

# THE ANATOMY OF SAUROSUCHUS GALILEI AND THE RELATIONSHIPS OF THE RAUISUCHID THECODONTS

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**ABSTRACT.** *Saurosuchus galilei* was a large quadrupedal carnivorous thecodont from the Ischigualasto Formation of western Argentina, which is of approximately Carnian age. Its skull anatomy indicates that it descended from an erythrosuchid type of primitive thecodont. *Saurosuchus*, together with *Luperosuchus*, *Prestosuchus*, *Ticinosuchus*, "*Mandasuchus*," and possibly some other less well known genera, form a well-defined lineage that can be traced throughout most of the Triassic. *Rauisuchus* is considered a member of the same family, and thus the earlier name *Rauisuchidae* is retained for the group. Two other thecodont lineages, the *Proterochampsidae* and the *Ornithosuchidae*, are traced throughout the Triassic. The relationships of the three families strongly suggest that they are independent derivations of the three Early Triassic primitive families. Dinosaur origins remain unclear. There is no good evidence for associating the *Rauisuchidae* with early dinosaurs; on the contrary, there is an unexplained time overlap of large carnivorous dinosaurs and thecodonts that have nearly identical adaptations.

## INTRODUCTION

*Saurosuchus galilei* is one of the 18 or more genera of reptiles found in the now legendary Ischigualasto Basin of western Argentina. Its significance for paleontologic studies lies in the excellent preservation of the material, particularly of the skull and tarsus, which makes possible the clarification of the anatomy of the closely related Brazilian thecodonts, and generally aids interpretation of the family *Rauisuchidae* on a worldwide basis. Together

with *Ticinosuchus* from the Middle Triassic of Switzerland, *Saurosuchus* provides a key for tracing a thecodont lineage that was world-wide in distribution throughout most of the Triassic Period.

Most of the specimens used for this study were collected in the Ischigualasto Formation by expeditions from the Instituto Miguel Lillo of Tucumán, Argentina. The first specimen was collected in 1959, under the direction of Dr. Osvaldo Reig. Subsequent expeditions, led by José Bonaparte, recovered parts of four additional individuals. From these various parts, most of the skeleton can be reconstructed, although the forelimb is not represented in any of the specimens.

*Saurosuchus* was one of the largest thecodonts of its time, and no doubt competed with the emerging dinosaurs for the large carnivore role. Thecodonts, of course, lost the competition, and contemporary dinosaurs, both saurischian and ornithischian, from the Ischigualasto Formation indicate that superior locomotion was a factor related to dinosaurian dominance. At present, although *Saurosuchus* appears to be the most advanced member of the family yet described, it is less progressive anatomically than its dinosaurian contemporaries. The lineage of *Saurosuchus* provides evidence to support the premise that progressive thecodonts were competitors rather than progenitors of the dinosaurs.

Abbreviations for the institutions referred to in this report are as follows:

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- PVL Instituto Miguel Lillo, Tucumán, Argentina  
 DGM Division of Mines and Geology, Brazil  
 T University of Tübingen, Germany  
 PIMZ Paleontological Institute, Zürich, Switzerland  
 MSJ Museum of Natural Sciences, San Juan, Argentina

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## Geologic Setting

The Ischigualasto Basin (Hoyada de Ischigualasto or Valle de la Luna) forms a depression on the western limb of a large syncline whose axis runs northwest-southeast. Differential erosion of the soft claystones of the Ischigualasto Formation created a prominent depression at the base of the cliff-forming red sandstones of the Los Colorados Formations (see Fig. 1). The Triassic sediments extend approximately one hundred kilometers, and are bounded on the south by the Valle Fértil mountains and on the north by the Sierra de Mas range. Within this area of outcrop there are numerous minor flexures, principally anticlines. One such saddle-shaped anticline divides the basin into a northern and southern portion; this division coincides with the boundary between the provinces

of San Juan and La Rioja. The southern, or San Juan, portion is the larger of the two and has produced most of the fossils known from the basin. East of the depression, the opposite limb of the large syncline has exposed the type area of the earlier Chañares Formation.

Interpretation of the time-stratigraphic relationships of the sedimentary units in the Ischigualasto basin has varied considerably. For many years the whole succession was considered "Rhaetic," or uppermost Triassic. With the discovery of vertebrate fossils that were more primitive than the classic Upper Triassic fauna, vertebrate paleontologists assigned the Ischigualasto Formation to the Middle Triassic. As new discoveries are being made a consensus is forming that the Ischigualasto Formation is most probably of Carnian age, possibly Late Ladinian, with the underlying Los Rastros Formation closely equivalent in time to the Santa Maria Formation of Brazil. (I have elsewhere summarized the various interpretations of the South American Triassic: Sill, 1969.)

Although the general geologic relationships between the various formations are quite straightforward, no attempt has yet been made to study sedimentary cycles within the Ischigualasto Formation, or to correlate the occurrence of specific fossils with different sedimentary regimes.

## TAXONOMY AND MORPHOLOGY

### Introduction

Taxonomic history of the Rausiuchidae began with Huene's work on the specimens he found in the Triassic of Brazil. In a short paper on thecodont relationships (Huene, 1936), he proposed the subfamily Rausiuchinae as a part of the family Stagonolepidae to include the genera *Rausiuchus* and *Prestosuchus* from Brazil. Later, (Huene, 1942) the group was elevated to familial rank and the genus *Rhadinosuchus*, also from the Triassic of Brazil, was included. At about the same time (Huene, 1938), he described *Stagono-*

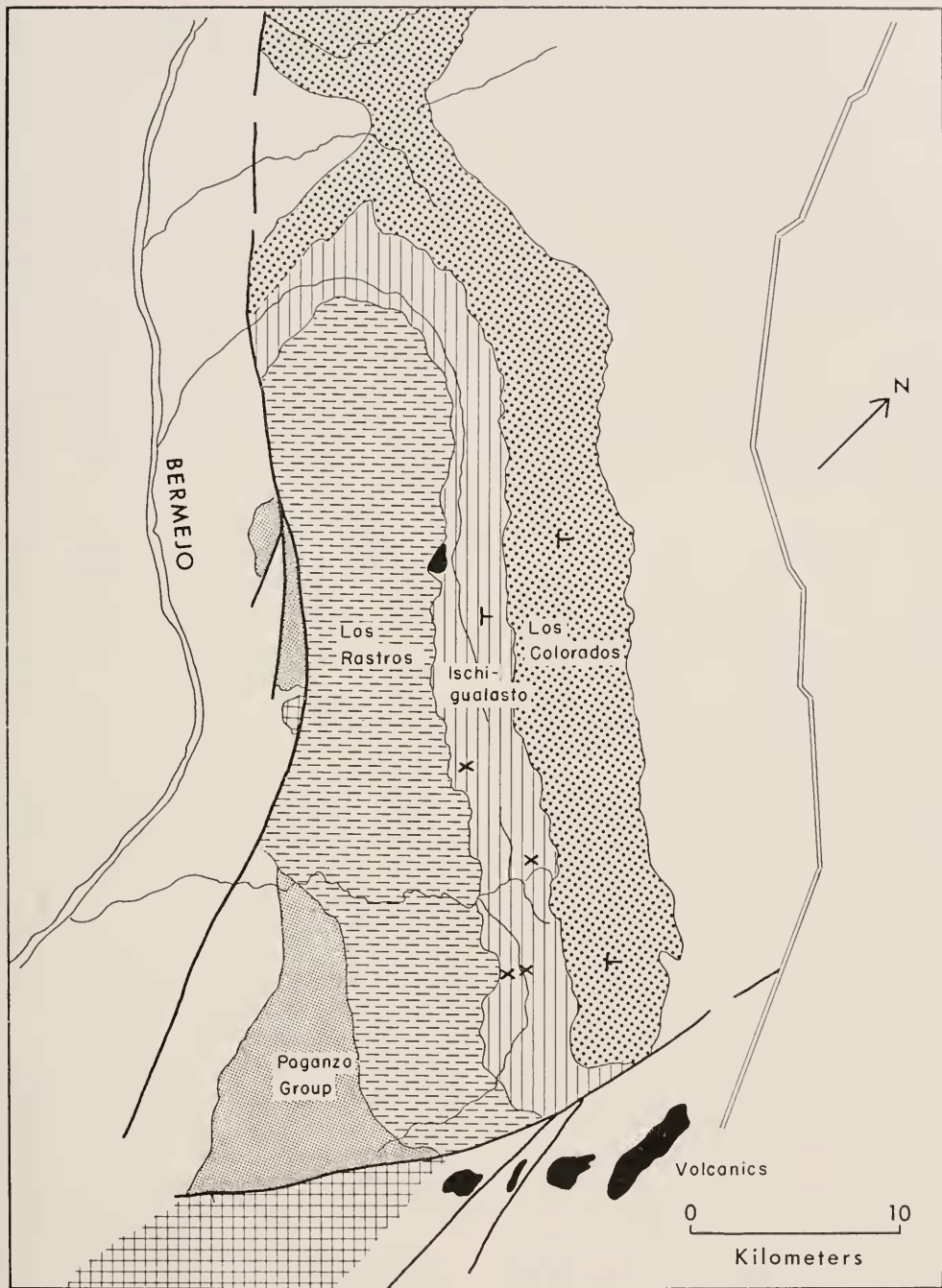


Figure 1. Generalized geologic map of the southern portion of the Ischigualasto Basin. X marks *Saurosuchus* localities.

*suchus* from the Manda Beds of East Africa and noted its similarity to the Brazilian forms. However, not until 1956 did Huene formally place *Stagonosuchus* in the family Raurisuchidae, at which time he also included a number of poorly known thecodonts that are no longer considered to be closely related to the family.

Since then, interpretations of the broader relationships of the Raurisuchidae have followed the general pattern of uncertainty that has been the hallmark of thecodont taxonomy. Huene (1956) continued to maintain the family in close association with the stagonolepid-aetosaurid groups and included in the family such diverse genera as *Cerritosaurus* and *Episcoposaurus*. Romer (1956) was the first to separate most of the genera of the Raurisuchidae from the armored thecodonts, and tentatively placed *Raurisuchus*, *Prestosuchus*, *Stagonosuchus*, *Rhadinosuchus*, and *Procerosuchus* in the Ornithosuchidae. Hoffstetter (1955) retained the family in the Stagonolepoidea, but removed *Stagonosuchus* to the Stagonolepidae. Reig (1961) presented a comprehensive review of the family and showed beyond reasonable doubt that the family Raurisuchidae should consist only of the genera *Raurisuchus*, *Prestosuchus*, *Stagonosuchus*, and the then recently discovered *Saurosuchus* from Ischigualasto. He also presented convincing evidence showing that the family is not closely related to the Stagonolepidae, and placed it in the "traditional" thecodont group which he termed Ornithosuchia (the equivalent of Pseudosuchia of most authors). Hughes (1963), on the other hand, tentatively placed *Raurisuchus* and *Saurosuchus* in the primitive thecodont group Proterosuchia as members of the Erythrosuchidae, a ranking that has not been accepted by the majority of paleontologists. *Ticinosuchus*, on the basis of a complete skeleton, was added to the family by Krebs (1965); its affinities with the other members of the family as described by Reig are evident. A further genus, *Luperosuchus*,

from the Chañares Formation, was added to the family by Romer (1971a), and a closely related form has recently been found in the Los Colorados Formation (Bonaparte, personal communication). These latter discoveries are especially significant, for they permit the *Saurosuchus* lineage to be traced through the major part of the Triassic in a single basin of deposition. Romer (1966) followed Hughes in tentatively associating *Raurisuchus* and *Saurosuchus* with the Erythrosuchidae, and adopted the term Prestosuchidae from Charig's unpublished thesis for the remaining genera *Prestosuchus*, *Procerosuchus*, "*Mandasuchus*"<sup>1</sup> and, tentatively, *Stagonosuchus*. However, he later (1968) replaced *Raurisuchus* and *Saurosuchus* with the above mentioned forms, but did not suppress Prestosuchidae. Meanwhile Prestosuchidae was carried on by Charig<sup>2</sup> (1967), who notes that the group is essentially the same as the Raurisuchidae of Huene (1942) but with the genus *Raurisuchus* excluded.

In a more recent work on thecodont taxonomy Romer (1972a) continued to use the family name Prestosuchidae on the grounds that *Raurisuchus* was too poorly known. However, he included *Raurisuchus* within the family Prestosuchidae (see Discussion with regard to the affinities of *Raurisuchus*).

Assignment of the Raurisuchidae to a suborder is difficult given the present unstable nature of thecodont taxonomy. Romer (1972a) places the family with the primitive thecodonts in the Proterosuchia; other authors, Charig (1967) and Bonaparte (1971) place it in the usual "catch-all" suborder Pseudosuchia. Raurisuchids certainly appear to have been derived from the erythrosuchid lineage of the Proterosuchia (see discussion on thecodont phylogeny),

<sup>1</sup> *Mandasuchus* is technically a *nomen nudum*, as it has never been described in print.

<sup>2</sup> In Charig's paper, origin of the Prestosuchidae was ascribed to Charig 1967. This paper has not been published. In an erratum, the family name was given as Romer 1966.



but they are much more specialized and progressive than any of its known members. On the other hand, they do not have a great deal in common with the "typical" ornithosuchid pseudosuchians. As thecodont relationships become more clearly understood, a new suborder will probably have to be erected for this and perhaps other lineages descended from the erythrosuchids, but at present such a step would be premature.

Discovery of nearly complete remains of *Ticinosuchus* and *Saurosuchus*, representing what appear to be the earliest and the latest members of the lineage so far described, has provided the means for an accurate characterization of the family. Basically, the new evidence tends to confirm the definitions of the family given by Krebs (1965) and by Reig (1961); Reig's paper provides an excellent summary of the taxonomic history of the family and of the Thecodontia in general.

The family may be defined as follows: Medium- to large-sized carnivorous quadrupedal thecodonts. Skull large, deep, orbit keyhole-shaped, large elongate antorbital fenestra, small crescent-shaped accessory antorbital fenestra present in some genera, teeth flattened, recurved, serrated. Pelvis triradiate, acetabulum closed, ischium elongated and rodlike, fused at the midline along most of its length. Femur long, slightly sigmoid, without a well-defined fourth trochanter. Calcaneum and astragalus articulate by a ball and socket joint, the socket on the calcaneum, the ball on the astragalus. Five digits, fifth metatarsal short and hooked. Many of these features are generalized characteristics of the primitive thecodonts which have been carried over in the family and are retained throughout their known history.

*Family distribution.* Middle and Late Triassic; Argentina, Brazil, East Africa, Switzerland, possibly China. Family *Rauisuchidae* Huene 1936 (as a subfamily); genera *Rauisuchus* Huene 1936 Brazil, *Prestosuchus* Huene 1936 Brazil, *Stagonosuchus*

Huene 1938 East Africa, *Saurosuchus* Reig 1959 Argentina, *Ticinosuchus* Krebs 1965 Switzerland, *Luperosuchus* Romer 1971 Argentina, "*Mandasuchus*" unpublished thesis Charig 1956. A number of additional genera are sometimes included in the family (see Romer, 1966 and 1972), but they are not well known. These additional genera are: *Cuyosuchus*, *Hoplitosaurus*, *Rhadinosuchus*, *Pallisteria*, *Spondylosoma*, *Procerosuchus*, *Fenhosuchus*.

### *Saurosuchus* Reig 1959

*Type species.* *Saurosuchus galilei*.

*Distribution.* Late Ladinian or Carnian, Ischigualasto Basin, Western Argentina.

*Diagnosis.* As for the species.

### *Saurosuchus galilei* Reig 1959

*Type.* PVL 2062, nearly complete skull, posteriormost portion missing.

*Hypodigm.* The type and: PVL 2198, partial maxilla, left ilium, both ischia, nine articulated dorsal vertebrae and fragments, part of the dermal armour, associated ribs and teeth. PVL 2557, two dorsal vertebrae, both sacrals, nine caudals, right ilium and ischium, partial pubis, parts of right femur, tibia, fibula, complete right tarsus and foot, associated ribs and chevrons. PVL 2267, poorly preserved partial ilium, partial femur, tibia, fibula, well-preserved tarsus, partial foot. PVL 2472, poorly preserved cervical vertebra, tibia, astragalus. MSJ 102, fragment of maxilla and lower jaw.

*Horizon.* Apparently all levels of the Ischigualasto Formation, San Juan province, Argentina. The five specimens of *Saurosuchus* were collected from four localities, all in the southern portion of the outcrop area. The type, PVL 2062, consists of a nearly complete skull and was found in the upper third of the strata. The more complete skeletons, PVL 2198 and PVL 2557, came from the middle part of the section, and the remaining two individuals, PVL 2267 and 2472, were found in the lower third of the strata, as was MSJ 102 (see map for specific localities).

*Emended diagnosis.* Large carnivorous thecodonts, up to six meters in length. Skull deep, elongate, finely sculptured, with keyhole-shaped orbit, large antorbital fenestra elongated anteriorly, small crescent-shaped accessory antorbital fenestra present between premaxilla and maxilla. Large elongate, nearly vertical external nares bordered only by premaxilla and nasal. Teeth robust, recurved, laterally compressed with serrate edges. Four teeth on premaxilla, ten on maxilla. Strong orbital arch formed by the frontal, small supratemporal fenestra lying in dorsal plane of the skull below the crest of the orbital arch. Vertebrae amphicoelous, spines broad and flat with prominent interspinous notch on anterior face. Cervicals apparently elongated, dorsals strongly compressed laterally, rib facets well separated and on different levels throughout column. Two sacral vertebrae. Shoulder girdle and forelimb unknown. Pelvis with closed acetabulum, pubis almost excluded. Ilium with broad brevis shelf, ischium long, rodlike, expanded at the tip and fused at the midline along most of its length. Femur slightly sigmoid, without a large greater trochanter, and with a small fourth trochanter. Fibula bears a prominent iliofibularis tubercle. Tarsus of the "crocodiloid" type, calcaneum bearing a large tuber and a prominent medial socket for articulation of the astragalar ball. Facets for articulation of the tibia and fibula close together. Fourth tarsal large, subtriangular with prominent rounded facet for articulation of fifth metatarsal. Five digits on foot, first two most robust, third is the longest, fifth is broad, flat, and oriented outward. Dermal armour present, two rows of small scutes along each side of most of the vertebral column, leaf-shaped and imbricating.

## General Description

### SKULL

*Cranium.* Cranial material is represented almost exclusively by the type, in which most of the dermal elements are preserved,

but the occipital region and braincase are lacking. A fragment of the right maxilla of PVL 2198 is identical to the corresponding region of the type and allows assignment of the specimen to the genus with a considerable degree of confidence. The lower jaw is known only from a fragment.

The skull is long, approximately 65 centimeters, triangular in shape, and sturdily constructed. The cranial table is high and narrow. Orbits are large, keyhole-shaped openings, of which the upper part is a well-defined circle high up the side of the skull. A large antorbital fenestra is present, subtriangular in shape and slightly smaller than the orbit. It is surrounded by a well-defined smooth border set in from the sculptured surface of the maxilla. An unexpected feature is the presence of a narrow accessory antorbital fenestra located between the maxilla and the premaxilla, extending from above the tooth-bearing surface to the posterior tip of the external nares.

Like the antorbital fenestra, the external nares are subtriangular in shape, relatively large, and situated principally in the vertical plane of the skull. Notable for their small size are the supratemporal fenestrae, which lie in the horizontal plane of the skull roof just behind and slightly below the heavy orbital arch. Only the anterior border of the infratemporal fenestra is preserved, but it indicates a triangular or subrectangular shape approximately the same size as the orbit.

The large size of the skull and its sturdy construction indicate that *Saurosuchus* was an active predator. Using the head size index of skull length to length of the presacral vertebral column, a value of either .27 or .34 is obtained, the latter calculated on the assumption that neck vertebrae were approximately the same length as the dorsals, while the smaller ratio assumes elongated cervicals. Both indices are in the range of the large predaceous dinosaurs; *Allosaurus* is .28, *Tyrannosaurus* is .41.

*Premaxilla.* Both premaxillae of the type are complete and well preserved. The main body of the bone is a massive rectangle from which a slender process extends upward and backward around the external naris to a long overlapping contact with a similar process of the nasal, and a second rodlike extension that forms the entire lower border of the naris and terminates wedged between the nasal and the maxilla. At its anterior border the premaxilla forms a straight vertical line from the tip of the naris to the first tooth position. Below the narial opening the bone swells to a thick, slightly undulating ridge that bears four large teeth. At the most anterior part, just above the tooth row, lie three foramina. No sculpturing is present. The rodlike process that forms the lower border of the naris is an isolated structure that separates the accessory antorbital fenestra and the external naris.

Medially, the premaxillae meet in a long sturdy symphysis. The alveolar margin is thick and slightly vaulted behind the first two teeth. Of the four teeth, the third is the largest. Two deep pits are present in the vaulted area, one beside the second tooth, the other between the third and the fourth. A large foramen is present above the third alveolus. The interalveolar septum between the third and fourth teeth is expanded on the lingual surface to form a small interdental plate.

Posteroventrally, a clearly defined suture is not present between the maxilla and the premaxilla, but above the thick tooth-bearing portion of the bone the accessory antorbital fenestra serves to separate the two elements.

*Maxilla.* The maxilla is a large platelike bone that slopes posteriad and upward from its suture with the premaxilla to meet the nasal and lacrimal dorsally and the jugal ventrally. It is deeply emarginated by the antorbital fenestra, around which runs a broad smooth shelf. Outside the shelf area the maxilla is heavily sculptured by an irregular network of grooves. It forms

TABLE 1. MEASUREMENTS OF THE SKULL (IN CENTIMETERS) OF *SAUROSUCHIUS GALILEI* BASED ON THE TYPE PVL 2062. NOTE, FURTHER PREPARATION HAS MODIFIED SOME OF THE MEASUREMENTS MADE BY REIG (1959) IN HIS PRELIMINARY ACCOUNT.

|  |                    |                     |
|--|--------------------|---------------------|
| Total length of the skull (estimated)  | 67                 |                     |
| Length from tip of snout to anterior border of the supratemporal fenestra                      | 54                 |                     |
| Length from lower anterior corner of infra-temporal fenestra to tip of snout                   | 47                 |                     |
| Diameter of the upper portion of the orbit   | 10                 |                     |
| Maximum height of the orbit  | 17                 |                     |
| Maximum length of the antorbital fenestra  | 19                 |                     |
| Maximum height of the antorbital fenestra  | 8                  |                     |
| Maximum length of the depression surrounding the antorbital fenestra                           | 21.5               |                     |
| Maximum height of the depression surrounding the antorbital fenestra                           | 10                 |                     |
| Maximum height of the skull between top of the rim of the orbit and bottom of jugal            | 20.5               |                     |
| Length of nasals along the midline   | 32                 |                     |
| Length of the premaxillary tooth row   | 9                  |                     |
| Length of the maxillary tooth row  | 27                 |                     |
| Length of the external naris   | 12                 |                     |
| Distance from tip of snout to anterior border of the antorbital fenestra                       | 21                 |                     |
| Width of skull across the supratemporal fenestrae  | 17                 |                     |
| Width of skull in front of the orbits  | 10                 |                     |
| Length of teeth alveoli  |                    |                     |
| Premaxilla   |                    |                     |
| 1.   | 1.5                |                     |
| 2.   | 1.5                |                     |
| 3.   | 2.0                |                     |
| 4.   | 1.3                |                     |
| Maxilla  |                    |                     |
| 1.   | 1.8                |                     |
| 2.   | 2.4                |                     |
| 3.   | 3.0                |                     |
| 4.   | 2.6                |                     |
| 5.   | 2.7                |                     |
| 6.   | 2.2                |                     |
| 7.   | 2.3                |                     |
| 8.   | 1.9                |                     |
| 9.   | 1.8                |                     |
| 10.  | 1.8                |                     |
| Length of maxillary teeth, left side, from lateral edge of the maxilla to the tip of the teeth |                    |                     |
| Tooth No.  | Anterior curvature | Posterior curvature |
| 3.   | 4.6                | 3.5                 |
| 5.   | 5.8                | 4.7                 |
| 6.   | 3.5                | 2.5                 |
| 7.   | 5.0                | 3.9                 |
| 8.   | 3.9                | 3.1                 |



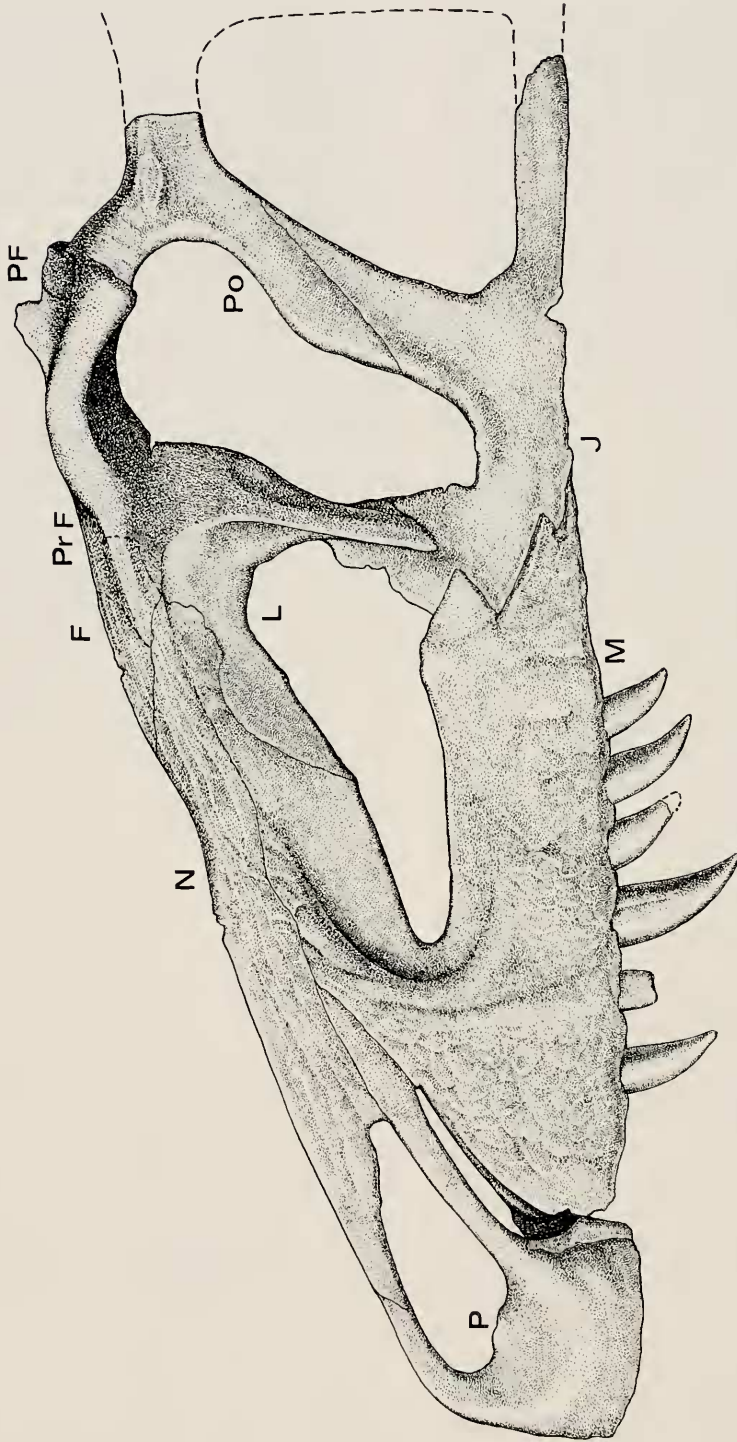


Figure 2. Lateral view of the skull of *Saurosuchus*. P—premaxilla, M—maxilla, N—nasal, J—jugal, F—frontal, L—lacrimal, PrF—prefrontal, PF—post-frontal, Po—postorbital.  $\times \frac{1}{4}$ .



the entire ventral, and half of the dorsal borders of the antorbital fenestra, meeting the lacrimal in a broad overlapping suture on the smooth shelf portion, and the jugal in a broad zig-zag digitate union. Ten teeth were present on the maxilla, of which seven were apparently functional at any one time. Numerous foramina are present on the lateral surface just above the tooth row.

On the medial surface the most prominent feature of the maxilla is the formation of the alveoli by large interdental plates. The plates are leaf-shaped extensions of the alveolar septa and slightly overlap one another at the middle of the tooth body. Above the plates a prominent groove runs to the dental lamina, which slopes downward posteriorly to terminate on the ventral surface of the maxilla just behind the last tooth. From the groove foramina representing the replacement teeth open directly above each tooth. This morphology apparently represents a standard pattern of tooth replacement, analyzed by Edmund (1957, 1960), in which the fibrous connective bone that surrounds the tooth is partially resorbed during the replacement process to form the shield-shaped interdental plates.

Above the tooth row, in the anterior portion of the maxilla, a massive buttress projects medially to meet the vomer and form part of the vault of the premaxillary chamber. Dorsally, on the medial surface, the maxilla terminates in a straight sloping contact with the nasal and the broad overlap of the lacrimal. Posteriorly the jugal is laminated to the maxilla just above the tooth row. A large maxillary foramen is present just anterior to the jugal suture midway between the tooth row and the ventral border of the antorbital fenestra, on the medial surface.

*Nasal.* Anteriorly, the nasal is a thin bar above the external naris overlapping the similar element of the premaxilla. From this position it broadens to a dorsal and component thickens considerably near its lateral plate of bone. Posteriorly the dorsal

union with the frontals, from .5 to 1.5 cm. The lateral component is not extensive and disappears entirely at the beginning of the antorbital fenestra. At their maximum width the joined nasals are approximately seven centimeters wide, an indication of the narrowness of the anterior portion of the skull. Sculpturing on the nasal is in the form of irregular longitudinal grooves. Union with the maxilla and lacrimal is in a straight sloping line. The suture with the frontal is an inverted V located at the level of the posterior border of the antorbital fenestra.

*Prefrontal.* The area corresponding to the prefrontal is badly fractured, but this element appears to be a small platelike bone lying in the horizontal plane above the lacrimal. It does not participate in the orbit, but sutures are difficult to distinguish.

*Lacrimal.* Most of the lacrimal lies in the depression surrounding the antorbital fenestra and is therefore completely smooth, as is that part of the maxilla that participates in the same depression. The lacrimal is an extensive thin plate, forming most of the smooth shelf around the upper part of the antorbital fenestra. Anteriorly it is overlapped by the maxilla. Posteriorly it forms a ventral prong that overlies the dorsal extension of the jugal to form the preorbital bar. The border between lacrimal and prefrontal is not discernible, but must lie in the zone behind the smooth depression of the fenestra. This area is thick and heavily sculptured, and from it arises a prominent lateral ridge that runs down the surface of the preorbital bar, terminating at the tip of the ventral prong of the bone. The lacrimal forms the upper third of the posterior border of the antorbital fenestra, and virtually all of the anterior border of the orbit. There is no definite lacrimal foramen, but a rounded depression is present on the ill-defined internal border between the lacrimal and the frontal. There is no transverse component of the lacrimal.

*Jugal.* The large skull openings of *Saurosuchus* have reduced the jugal to a hori-

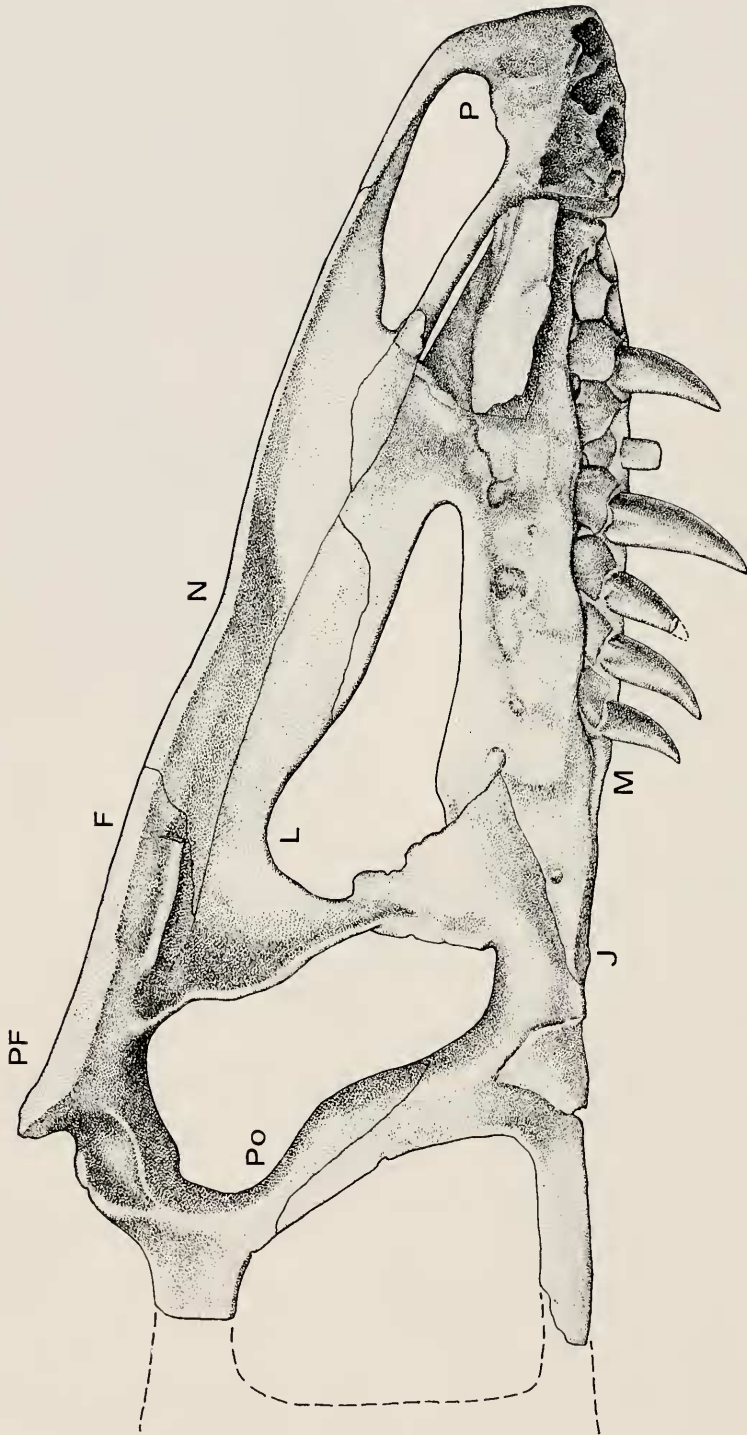


Figure 3. Medial view of the skull of *Saurosuchus*. P—premaxilla, M—maxilla, N—nasal, J—jugal, F—frontal, L—lacrimal, PF—postfrontal, Po—postorbital.  $\times \frac{1}{4}$ .

zontal rod with two dorsal prongs projecting upwards to form parts of the pre- and postorbital bars. It is most expanded anteriorly where it is platelike and overlapped by the maxilla in a prominent zig-zag suture. Immediately behind this union, the dorsal projection of the preorbital bar reaches up medial to the narrow ridge of the lacrimal. Behind the orbit the second prong of the jugal extends upward and backward to form a strong, sloping, abutted contact with the ventral expression of the postorbital. At the ventral border of the infratemporal fenestra, the jugal is a relatively narrow uniform bone. It thins out to a fine edge on its lateral surface, showing clearly the area where it was overlapped by the quadratojugal. Sculpturing is present only in the anterior portion of the bone, where it meets the maxilla, and even that is light. Only the ventralmost part of the orbit is formed by the jugal, but it constitutes nearly all of the anterior border of the infratemporal fenestra. Directly below the postorbital bar there is an outward bulge in the jugal, forming a distinct pocket on the internal surface, possibly the contact for the ectopterygoid.

*Frontal.* The frontal is a thick strong bone dominated by the massive supra-orbital arch. Medially it curves down from the arch to the midline where its posterior portion meets the anterior projection of the parietal. Anteriorly it joins the nasal and prefrontal in a zig-zag suture. Sculpturing is present, principally on the arch, and is of the pit and groove variety. The thickest part of the frontal is the area of the midline, which in the type is two centimeters deep. Internally there does not appear to be an interorbital septum, but the orbit is well defined by the medial continuation of the orbital arch. Anteriorly the arch forms the previously mentioned pocket at its junction with the lacrimal. Anterior to the orbit the frontal thins to slightly over one centimeter in thickness, and bears a downward-projecting ridge near the midline. This ridge, presumably the border of the

olfactory tract, is eight millimeters high at its maximum and tapers off to the level of the bone at the anterior end of the frontal. Behind the orbit, at the junction of the frontal, parietal, postfrontal, and postorbital, a prominent circular pocket is present. This most probably received the anterior process of the laterosphenoid.

*Postfrontal.* This is a small semicircular bone lying on the dorsolateral surface of the skull between the frontal and the postorbital. It does not enter into the supratemporal fenestra. On the ventral surface of the skull it is not possible to distinguish the borders of the postfrontal.

*Postorbital.* The postorbital forms nearly all of the posterior border of the orbit, and the upper third of the anterior border of the infratemporal fenestra. Dorsally, just behind the orbital arch, it bears a prominent, sculptured tuberosity. Ventrally, it meets the ascending process of the jugal in a long diagonal contact. The anterior border of the postorbital bar is emarginated and beveled at the delimitation of the circular part of the "keyhole" orbit. On the cranial table the postorbital forms most of the lateral and anterior border of the small supratemporal fenestra. A well-defined, smooth margin surrounds this fenestra, otherwise the upper region of the postorbital is sculptured by linear grooves. Internally, the anteromedial portion of the postorbital forms the rear part of the socket for the laterosphenoid articulation. The posterior part of the postorbital is not preserved in the type.

Nothing remains of the cranial table behind the frontal and postorbital bones in the available material.

#### PALATAL COMPLEX

Palatal remains of *Saurosuchus* are not well preserved, but allow reconstruction of the major features. A primitive character of the palate is the long triangular interpterygoid vacuity. The internal nares are somewhat displaced toward the rear and close to the sides of the maxillae. No traces

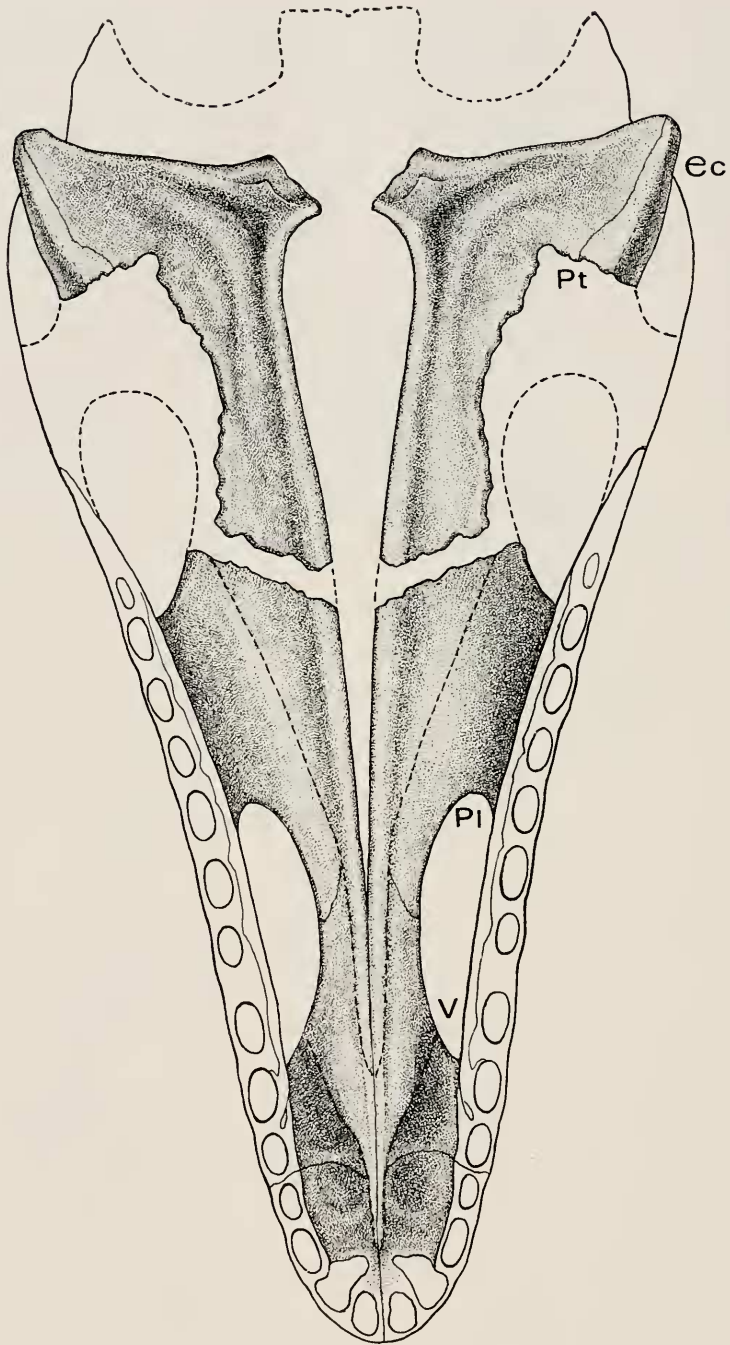


Figure 4. Palatal view of the skull of *Saurosuchus*. Ec—ectopterygoid, Pt—pterygoid, PI—palatine, V—vomer.  $\times \frac{1}{4}$ .



of teeth are found on the palatine or on the pterygoid. Although crushed, the palate appears to have formed a deep vault rather than a shelf. The basieranium is not known.

*Pterygoid.* As usual, the pterygoid is the largest of the palatal bones, and is divided into the customary three components: flange, palatal, and quadrate rami. The palatine ramus consists of a broad thin plate of bone that extends forward from the base of the flange portion and narrows anteriorly to a V-shaped ridge that meets the vomer near the midline. The medial border of the pterygoid is formed by a rounded ridge and steep shelf of bone that form the edge of the interpterygoid fenestra. Only at the anteriormost tip do the pterygoids join at the midline. On the dorsal surface of the palatal ramus a deep groove is present just lateral to the wall of the interpterygoid vacuity. This groove may continue onto the vomer. The flange portion of the pterygoid is massively constructed, and bears a thick, rounded posterior border that curves out to form the "wing." Where the wing meets the heavy ridge that borders the interpterygoid fenestra a deep pocket is formed. Posteromedial to this pocket lies a thick remnant of the basiptyergoid articular bar. Anteriorly the flange thins considerably, becoming the same thickness as the palatine. At the posterior margin the flange is 15 mm thick, while anteriorly it is only 4 mm. The angle of inclination of the flange is approximately 45 degrees.

*Ectopterygoid.* Only the massive portion of the ectopterygoid that forms the lateral border of the pterygoid flange is preserved. This portion forms a strong buttress along the entire lateral edge of the pterygoid "wing." There is no identifiable scar on the maxillae or jugal to indicate the articulation of the ectopterygoid, although it seems probable that the bulge just below the postorbital bar was for reception of the ectopterygoid strut. The massive nature of the preserved portion of the bone indi-

cates that the ectopterygoid served to strengthen the lateral part of the pterygoid.

*Palatine.* As preserved, the palatine is a thin plate, not possessed of unusual characteristics. Anteriorly it forms the posterior half of the internal naris; the suture with the vomer is well preserved. Laterally it is applied to the side of the maxilla, opening posteriorly into the pterygoid fenestra. The medial border is not well preserved, but appears to have been of the usual platelike contact with the pterygoid.

*Vomer.* The vomer is poorly preserved and represented only by a distorted and ill-defined mass of bone anterior to the internal nares. As near as can be determined, the vomer formed the anterior half of the internal naris, above which it expanded considerably in the form of a laminar sheet of bone applied to the medial side of the massive maxillary buttress. Possibly, a portion of the vomer behind the maxilla formed a secondary buttress behind the laminar part.

*Dentition.* Most of the 14 sturdy teeth in the upper jaw are of equal or nearly equal size. In the premaxilla the teeth are not preserved, but to judge from the size of the alveoli, the first and fourth teeth are slightly smaller than the second and third. In the maxilla, the last three teeth show a slight reduction in size compared with the anterior ones. All of the maxillary alveoli show the presence of functional teeth, with the possible exception of the first two, although at least two and possibly three growth stages are represented. The third, fifth, and seventh teeth are the largest, with the fifth slightly larger than the others. The fourth, sixth, and eighth are approximately the same size. The ninth and tenth teeth are broken off at the alveolar border, but were similar to the eighth in size. All of the teeth are of similar shape, heavily constructed, laterally compressed, sharply pointed, and recurved. The last three or four of the maxillary series seem to be more strongly recurved than the anterior members, but this may be due to deformation.

Roots of the teeth are approximately twice as long as the crown. Near the alveolar margin, the teeth are much more compressed and elongate than in the main body of the crown, and on the fully erupted teeth a slight depression is present on the lingual face of the tooth near the margin formed by the alveolar septum (see Plate 1). The teeth are essentially symmetrical, but the plane of symmetry, taken between the anterior and posterior serrations, is slightly rotated anteromedially-posterolaterally. Enamel on the crown is thin and not striated.

Serrations are present on the distal three-quarters of the anterior edge and along all of the posterior margin. However, this condition can be fully appreciated only on the fully erupted teeth; in those teeth that have not reached maturity the serrations continue to the alveolus. Form of the serrations is the same on both edges; they consist of simple crosscuts perpendicular to the long axis of the tooth. Density of the serrations is 12-14 per 5 mm, and is the same on both the anterior and posterior edges. There are no wear facets on the teeth, although the larger ones have a somewhat more rounded apex.

#### AXIAL SKELETON

The exact number of presacral vertebrae is not known. Two vertebral series are preserved, PVL 2198 and PVL 2557. The former consists of nine dorsals, all of which bore ribs; the latter series is from the sacral and caudal region and does not duplicate any of the vertebrae of the PVL 2198 series. In PVL 2557 the first two presacrals are preserved and show that ribs were not present on these. As the anterior members of the PVL 2198 series do not show characteristics of cervical vertebrae, it seems reasonable to assume that not more than two vertebrae represent the gap between the presacrals of the two series. Assuming the usual presence of seven or eight cervicals, the vertebral count would fall into the 23 to 25 characteristic of archosaurs. In general, structure of the vertebral column

parallels the development found in some prosauropods, and seems to be related to size.

*Cervical vertebrae.* Only one cervical is known, PVL 2472. It is poorly preserved and of questionable reference to *Saurosuchus*. It was found in association with a tibia and astragalus, also poorly preserved, that appear to be identical to those of PVL 2267. However, the unusual features of the vertebrae warrant its inclusion in this study even though its association with *Saurosuchus* is not completely reliable. Only the centrum is preserved; it is an elongated, flattened structure generally constricted in the middle. The anterior (?) face is strongly concave and bears a protruding lower margin that would seem to indicate a cervical flexure. The rear (?) surface is only slightly concave. There is no keel. In the middle portion, the body of the centrum is not only constricted laterally, but is also greatly flattened, which transforms the whole into a very lightly built structure. Prominent pleurocoels are present just behind the flared articulating surfaces. Thus the lateral border of the centrum is almost a horizontal plate that curves inward to the narrow waist (see Fig. 5). The characteristics of the vertebrae represent an early development of a strong, lightweight support for the cervical region. As such it is compatible with the dorsal vertebrae of PVL 2198, but the flatness and presence of pleurocoels are not found on any of the known dorsal vertebrae. This condition creates an element of doubt about the affinity of this strange cervical. Measurements are as follows: length, 18 cm; width of the anterior surface, 11 cm; width of the constricted waist, 4 cm; and approximate height at waist, 2 cm.

*Dorsal vertebrae.* Vertebrae of the dorsal series are represented by the first two presacrals of PVL 2557 and by nine articulated members of PVL 2198. The anterior members of the PVL 2198 series are poorly preserved. The most striking feature of the *Saurosuchus* vertebrae is the reduction of



A



B



C

Plate 1. A. Type of Skull of *Saurosuchus*, PVL 2062.  $\times \frac{1}{8}$ . B. Lingual view of left maxilla, note interdigital plates.  $\times 1$ . C. Enlarged view of a recently erupted tooth, showing serrations on the posterior edge.  $\times 8$ .



TABLE 2. MEASUREMENTS OF THE VERTEBRAL COLUMN OF *SAUROSUCHUS GALILEI* (IN CENTIMETERS).

| PVL 2472 cervical (?)  |  |             |           |          |       |       |
|--|--|-------------|-----------|----------|-------|-------|
| Maximum length   |  |             |           |          | 20.0  |       |
| Transverse width of posterior face                             |  |             |           |          | 10.5  |       |
| Transverse width of anterior face                              |  |             |           |          | 9.0   |       |
| Minimum width of constricted waist measured on ventral surface |  |             |           |          | 4.0   |       |
| Height of anterior face  |  |             |           |          | 5.3   |       |
| Height of centrum body at waist                                |  |             |           |          | 2.0   |       |
| Dorsal vertebrae PVL 2198                                      |  | Anterior    | Posterior |          |       |       |
| Maximum length of centrum                                      |  | 7.5         |           |          | 8.5   |       |
| Height of anterior rim   |  | —           |           |          | 8.7   |       |
| Width of anterior rim  |  | —           |           |          | 7.2   |       |
| Width of posterior rim   |  | 6.0         |           |          | —     |       |
| Total height of vertebrae                                      |  | 20.0        |           |          | 22.0  |       |
| Minimum width of constricted waist                             |  | 1.2         |           |          | 1.3   |       |
| Lateral extension of transverse process from the midline       |  | 5.5         |           |          | 4.8   |       |
| Width of neural spine table                                    |  | 3.0         |           |          | 2.4   |       |
| Diameter of parapophysis                                       |  | 2.5         |           |          | 2.5   |       |
| Diameter of diapophysis  |  | 2.7         |           |          | 2.7   |       |
| Height of neural arch above centrum                            |  | 12.6        |           |          | 13.0  |       |
| Lumbar and sacral vertebrae PVL 2557                           |  | Presacral 1 | Sacral 1  | Sacral 2 |       |       |
| Length of centrum  |  | 9.0         | 10.5      |          | 10.0  |       |
| Height posterior rim   |  | 12.0        | 9.5       |          | 10.0  |       |
| Width posterior rim  |  | 10.5        | 10.0      |          | 8.5   |       |
| Height anterior rim  |  | —           | 11.0      |          | 9.5   |       |
| Width anterior rim   |  | —           | 12.0      |          | 10.0  |       |
| Minimum width of constricted waist                             |  | 4.0         | 3.7       |          | 3.1   |       |
| Width of neural spine table                                    |  | 4.5         | 3.6       |          | —     |       |
| Height of neural arch above centrum                            |  | 17.6        | 19.5      |          | —     |       |
| Total height of vertebrae                                      |  | 28.0        | 29.5      |          | —     |       |
| Caudal vertebrae PVL 2557                                      |  | Caudal 3    | Caudal 9  |          |       |       |
| Length of centrum  |  | 8.0         |           |          | 7.5   |       |
| Height posterior rim   |  | 9.5         |           |          | 7.0   |       |
| Height anterior rim  |  | 9.0         |           |          | 7.0   |       |
| Width anterior rim   |  | 9.0         |           |          | 6.0   |       |
| Width posterior rim  |  | 9.0         |           |          | 6.0   |       |
| Minimum width of constricted waist                             |  | 3.9         |           |          | 2.3   |       |
| Width of transverse process from midline                       |  | 11.5        |           |          | 7.0   |       |
| Chevrons PVL 2557  |  | No. 1       | No. 2     | No. 3    | No. 4 | No. 5 |
| Length   |  | 18.0        | 21.0      | 21.5     | 21.2  | 18.5  |
| Width between articulations                                    |  | 7.5         | 7.5       | 6.7      | 6.2   | 6.0   |
| Width of articular facets                                      |  | 4.0         | 4.0       | 4.0      | 3.0   | 2.5   |
| Length from facet to fusion with opposite side                 |  | 4.5         | 3.8       | 4.0      | 3.5   | 3.2   |

the centrum to a thin vertical plate between the flared rims. This condition is not as well developed in other thecodonts and seems to be a unique weight-reduction

specialization of the genus. Another notable feature of the dorsals is the complete separation between the diapophysis and the parapophysis along the entire known series;



the latter is always found on the neural arch, never on the centrum. Transverse processes are larger in the anterior region than in the posterior, but all are rather short and stubby. The neural arches sit high on the centra and bear flat rectangular spines that are not inclined posteriorly. Size and shape of the vertebrae appear to be uniform throughout the series. All centra are uniformly amphicoelus and do not bear keels. Morphologic changes along the series are not prominent and consist principally of the reduction of the transverse processes in the lumbar region.

In end view the centra are oval-shaped with the long axis in the vertical plane. The rims are flared and rounded, not beveled. Reduction of the body of the centrum took place by expansion towards the rims of the common "hour-glass" constriction. The results are a steeper angle of the constriction behind the rims and the formation of a narrow plate between them (see Fig. 6). No ridges, rugosities or excavations are present on the body of the centrum. Length of the centrum is 7 to 8 cm, width 6 to 7 cm, height is around 9 cm. The body of the centrum expands slightly to receive the neural arch and form the floor of the neural canal.

The neural arch is a large structure that sits high up on the centrum. Contact with the centrum is a simple butt union, without the formation of pedicels. Prezygapophyses are not well preserved, but form short processes that sweep forward on either side of the prominent interspinous notch of the neural spine, just above the articular facet for the capitulum. Apparently the prezygapophyses did not overhang the border of the centrum. The postzygapophyses lie on the same level as the transverse process and are formed from lateral expansions that diverge from the base of the neural spine, creating a wedge-shaped cleft behind it. The zygapophyseal facets are relatively small smooth areas facing downward with a slight inclination toward the midline.

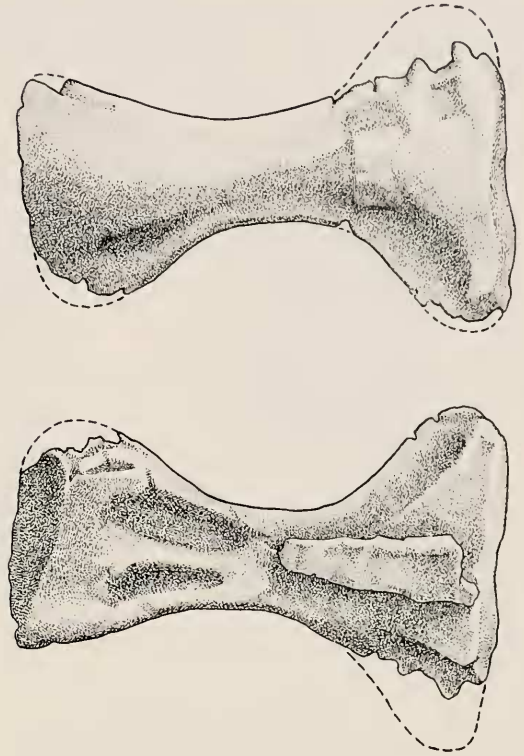


Figure 5. Supposed cervical vertebra of *Saurosuchus*. Top, ventral, Bottom, dorsal.  $\times \frac{1}{4}$ .

Rib articulations are restricted entirely to the neural arch. The parapophysis is a round facet on the anterior vertebrae of the dorsal series, but becomes laterally expanded into a peduncle on the posterior vertebrae. On all of the dorsals the parapophysis lies below and in front of the transverse process. These processes are short and robust; those of the shoulder region are larger than those of the lumbar series and project posteriorly approximately 30 to 45 degrees. The diapophysis forms as an expanded foot at the tip of the transverse process. On the anterior dorsals this expansion is considerably larger than the parapophyseal facet, while in the lumbar region it is of the same size. A notable feature of the transverse process is the presence of strutlike ridges on the under-

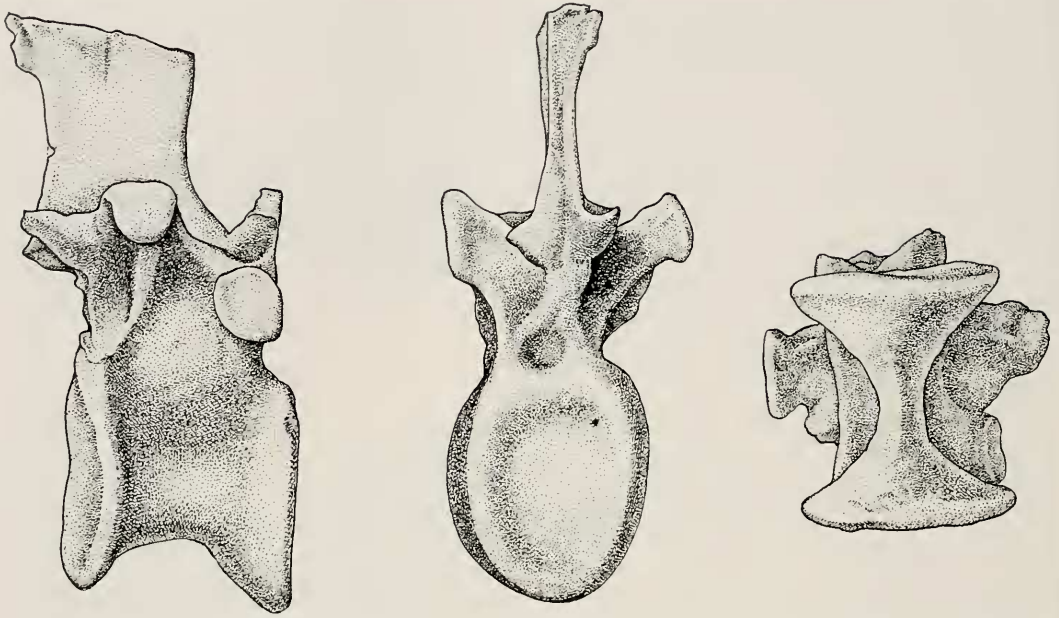


Figure 6. Three views of a dorsal vertebra of *Saurosuchus*. Left, right lateral; middle, posterior; right, ventral.  $\times 1/4$ .

side and edges. In the shoulder region, where the transverse process is largest, four struts are present. One extends to the prezygapophysis, another to the postzygapophysis, a third down to the parapophysis, and a fourth down and back to the rim of the centrum. All of the ridges extend the entire length of the transverse process, and form a strong supporting structure. In the posterior dorsals the strut structure is modified by a reduction to three struts. The parapophysis has moved slightly dorsal, almost to the level of the prezygapophysis and the transverse process is smaller. Only one ridge is present in the anterior portion, extending from the transverse process to the parapophysis. The shorter transverse process and the lateral expanded parapophysis change the aspect of the supporting strut from that of a ridge to a sheet of bone (see Fig. 6).

The neural spine on all of the dorsal vertebrae is a robust rectangular blade, slightly higher than the centrum. As well

as can be determined, the blade is not inclined posteriorly on any of the vertebrae. On its dorsal surface the spine is expanded into a spine table, presumably for the attachment of dermal armour. At the anterior and posterior borders the spine does not attenuate, but bears prominent grooves for the interspinalis musculature. On the leading edge the groove occupies the lower half of the length and is deeper at the base. The groove on the posterior margin is shallower but extends the entire length of the blade.

A distinct lumbar region was present in *Saurosuchus*, but it is not possible to determine the number of vertebrae involved. Specimen PVL 2557 has preserved the two vertebrae immediately anterior to the sacrum, and these vary from the other dorsals principally in their lack of normal ribs. It is not possible to determine whether the short downcurved processes are ribs or transverse processes. They appear to be transverse processes, arising from the same

position on the neural arches as those of the anterior dorsals. The processes are oval in cross section and heavily constructed. Their origin on the arch is considerably broader than that of the dorsals of PVL 2198. From the arch they curve slightly forward, then strongly downward.

*Sacral vertebrae.* The sacral vertebrae are known exclusively from the well-preserved representatives of PVL 2557. Two sacrals are present in *Saurosuchus*. The centra are slightly more elongate than the other dorsals, but otherwise are not different. The sacrals are not fused, but there is a considerable reduction of the rims where the two meet, with the posterior rim of the first sacral flared out at the sides and a corresponding reduction and slight forward extension of the anterior rim of the second sacral. This imparts a slightly V-shaped configuration to the union between the two vertebrae. This condition is repeated in the junction between the last sacral and the first caudal. Such a union must have essentially immobilized the three vertebrae involved, providing a partial substitute for the fusion of the sacrals. The transverse processes of the first caudal vertebrae are not preserved, so it is not possible to determine if it participated in supporting the pelvis. Position and shape of the transverse processes of the sacrals are essentially of the type found in primitive archosaurs; the first is large, oval-shaped, and positioned near the anterior border of the centrum, while the second is more crescent-shaped and arises from the center of the centrum. Both are impressive structures, greatly enlarged and heavily constructed.

Neural spines and arches of the sacral vertebrae are not significantly different from those of the presacrals that form the lumbar region. The spines are heavily constructed and expanded, but form a well-matched series with those of the lumbar. The same is true for the neural arches.

It should be pointed out that the vertebrae of specimen PVL 2557 do not have the

centra constricted nearly as much as those of specimen PVL 2198. Whether this difference is due to the difference in size between the two animals (PVL 2557 is considerably larger than PVL 2198) or to their different positions in the vertebral column cannot be ascertained.

*Caudal vertebrae.* In general the caudals of *Saurosuchus* are of shorter length than the other vertebrae, and have large rounded rims. The first three caudals do not bear chevrons. Diameter of the centra of the first five caudals is essentially equal to that of the sacrals. Beginning with the sixth caudal, there is a gradual reduction in size. Rims of all of the caudal vertebrae are broad and rounded compared to the somewhat thinner rims of the other vertebrae. The area between the rims is not reduced as in the dorsals; the centra are more "typical" in their squat rounded shape. Beginning with the seventh caudal, a slight groove appears on the ventral surface of the centrum. At the eighth or ninth the shape of the centrum changes to the more elongate and spool-like shape characteristic of tail vertebrae in general. Large lateral processes are present on the nine articulated caudals preserved in specimen PVL 2557. The processes of the first four or five caudals are large bladelike structures that extend outward and backward from the level of the dorsal surface of the centra. In caudals numbers six and seven, the outward extensions of the processes are greatly reduced, but they retain the blade shape. In caudals eight and nine, the lateral process loses the bladelike expansion and becomes a simple short lateral process.

Neural spines of the first four caudals are large, cover the entire length of the centrum, and in general are like those of the dorsals. Beginning with the fifth caudal there is a relatively sharp reduction in the anteroposterior length, and in the height of the spine. The spine becomes more inclined caudad and develops a more prominent interligamentum cleft in the anterior border near the base. The sides of the cleft



TABLE 3. MEASUREMENTS OF THE PELVIS OF *SAUROSUCHUS GALILEI* (IN CENTIMETERS).

|  | PVL 2198 | PVL 2557 |
|--|----------|----------|
| Ilium  |          |          |
| Length along dorsal border                           | 36.0     | 41.0     |
| Length of anterior spine from the ventral curvature  | 4.2      | 6.5      |
| Length of posterior spine from the ventral curvature | 17.0     | 23.5     |
| Height of dorsal border above acetabulum             | 6.5      | 10.5     |
| Maximum height of ilium                              | 23.5     | 29.0     |
| Width of dorsal border                               | 1.8      | 2.1      |
| Ischium  |          |          |
| Total length along curvature                         | 42.5     | 50.0     |
| Width of shaft                                       | 3.7      | 4.1      |
| Height of shaft                                      | 3.9      | 4.6      |
| Height of terminal expansion                         | 5.3      | 9.3      |
| Width of terminal expansion                          | 5.9      | 6.1      |

develop progressively into prominent ridges that sweep forward to form the prezygapophyses. Position of the zygapophyses undergoes a slight progressive shift towards the front; the prezygapophysis begins to overhang the centrum and is accompanied by a corresponding anterior displacement in the postzygapophysis.

*Chevrons.* Chevron bones first appear on the fourth caudal. The first four chevrons are Y-shaped and bear large disclike pedicels for articulation with the vertebrae. The arms of the "Y" become progressively closer together until they join at the fifth chevron (eighth caudal), leaving a small opening of which only a vestige remains in the sixth chevron (ninth caudal). Construction of the chevrons is simple and not unusual; the expanded pedicel is followed by a long sturdy shaft fused with its opposite just below the centrum. A slight ridge is present on the posterior surface of the shaft. The six preserved chevrons are all approximately the same length (equal to the total height of the vertebrae) and are strongly inclined caudad.

*Ribs.* Few ribs are preserved. Those available are fragmentary and are covered with a thick iron-rich matrix. They appear to be heavily constructed, thick-bodied, and with a prominent ridge on the upper third

of the anterior edge. The posterior surface (at least in the proximal section) is flat with a slight depression down the middle. Rib articulations appear to be well ossified. As may be expected, the largest ribs were the anterior members (size inferred from the relative size of the articular surfaces on the vertebrae).

#### APPENDICULAR SKELETON

*Pelvic girdle.* The pelvis of *Saurosuchus* is well represented except for the distal portion of the pubis. Elements available are: left ilium and paired ischia of PVL 2198; right ilium, complete right and partial left ischia of PVL 2557; and a poorly preserved fragmented ilium of PVL 2267. The proximal portion of the right pubis of PVL 2557 is articulated with the ilium of that specimen.

The usual elements of the pelvis were present, in typical triradiate forms. There is no indication of perforation of the acetabulum. A notable feature of the pelvis, apparently common to the Rauisuchidae, is the high position of the pubic articulation and the limited participation of this element in the acetabulum.

*Ilium.* Two major structural divisions are present on the ilium; the acetabulum and the iliac blade. Most of the ilium is



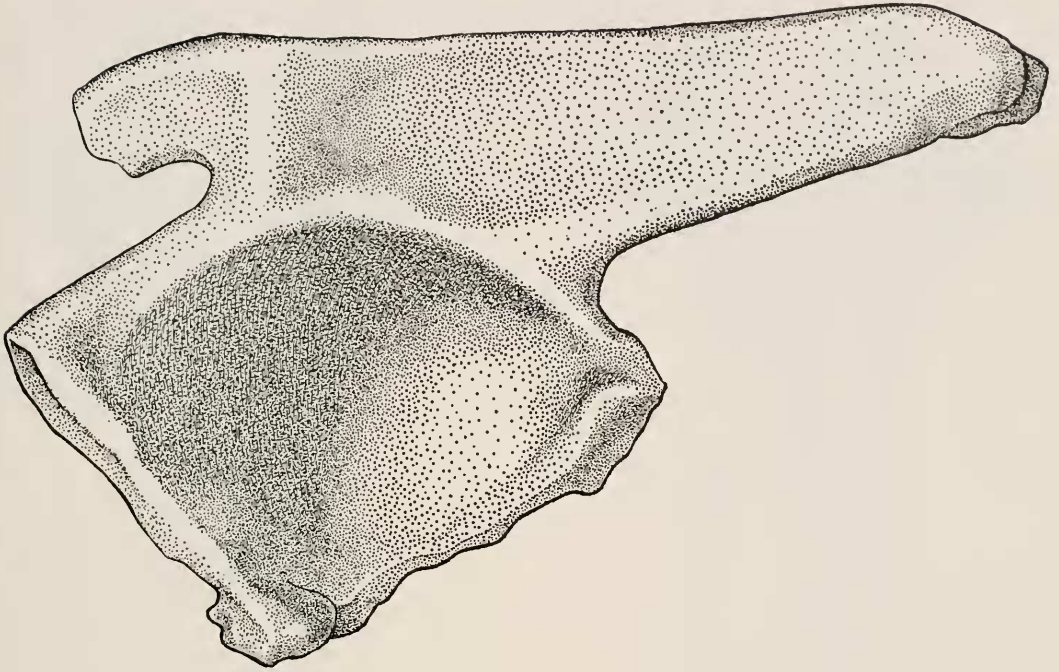


Figure 7. Ilium of *Saurosuchus*.  $\times \frac{1}{4}$ .

incorporated into the acetabulum, which is a large deep depression that faces slightly downwards. The dorsal margin of the acetabulum is formed by a thick lateral flange positioned just below the anterior emargination of the iliac blade. Ventrally the acetabulum wall thins considerably at its borders with the ischium and pubis. Anteriorly it expands transversely where it meets the dorsal border of the pubis, below which the bone thins, presenting a teardrop shape in cross section. A notable feature of the ilium is its articulation with the pubis and ischium; the suture of the pubis occupies nearly all of the anterior border, starting from a level almost at the dorsal border of the acetabulum, whereas the ischium meets the ilium more in the ventral plane. The ilium is not constricted above the acetabulum. Rather, the anterior origin of the iliac blade arises from an emargination immediately above the thick dorsal margin of the acetabulum, while the

posterior portion of the blade sweeps upward and backwards from a level slightly above the midline of the acetabulum. The anterior tip of the blade is short and thick; it does not reach the anterior border of the acetabulum. The posterior portion of the blade consists of three prominent elements: 1) a rounded dorsal ridge, 2) a horizontal shelf on the medial side, midway between the dorsal and ventral borders, and 3) the very thick rounded ventral border of the blade. The internal shelf corresponds to the structure termed "brevis shelf" by Romer (1927) and originates just behind the acetabulum, becoming considerably heavier and thicker at the terminal end of the blade. At its posterior tip the iliac blade is heavily constructed with the brevis shelf lying perpendicular to the blade. Rugosities present in the tip region indicate that it was probably continued in cartilage. Facets for the sacral ribs lie just above the level of the acetabulum. Total

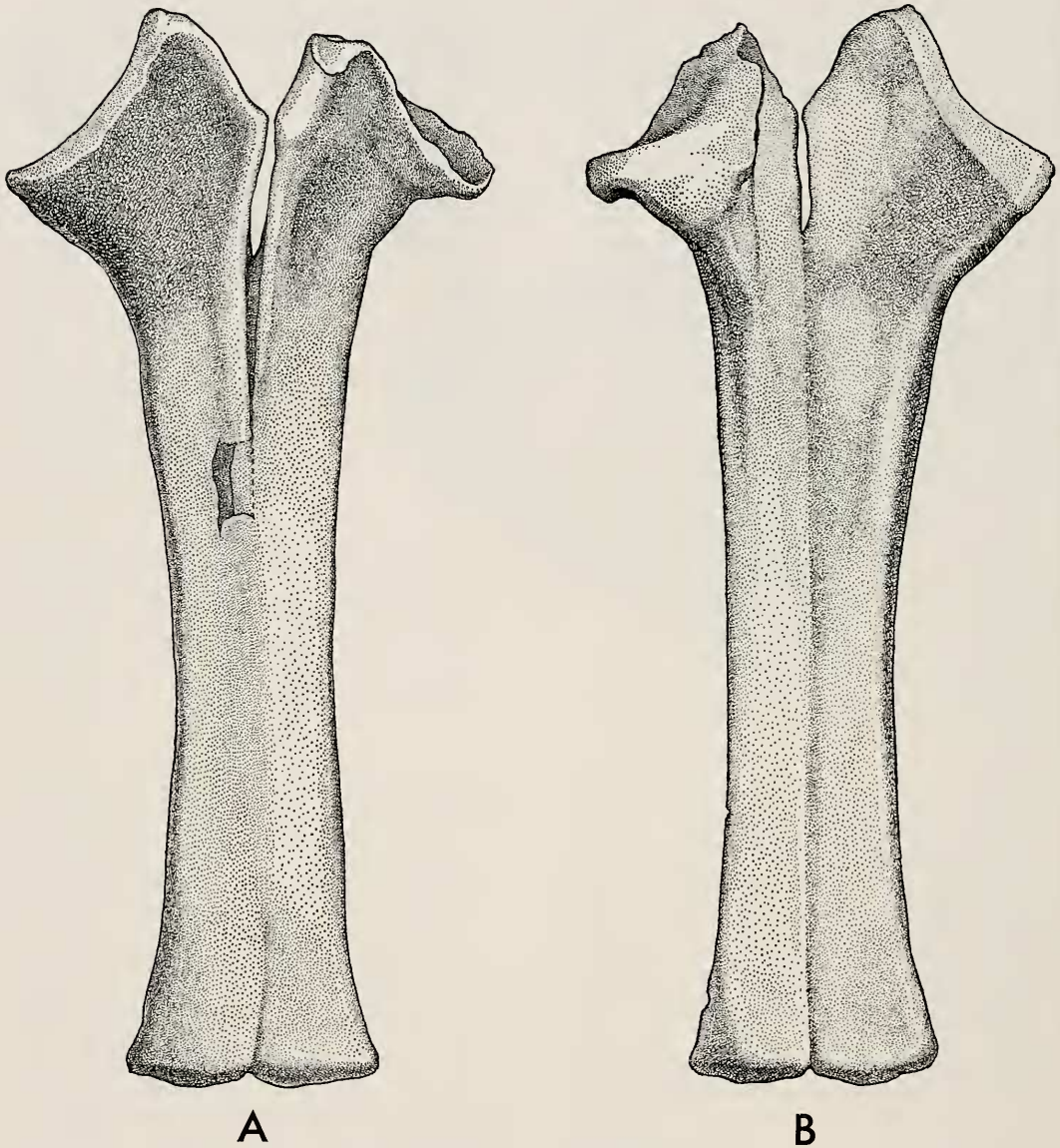


Figure 8. Two views of the paired ischia of *Saurosuchus*. A, ventral; B, dorsal.  $\times 14$ .

length along the dorsal border of PVL 2198 is 36 cm of which 16.5 lie below the acetabular rim. Thus the blade above the acetabulum is only 6 cm high.

*Ischium.* The ischium of *Saurosuchus* consists of a broad flange followed by a relatively long shaft that bears a mild terminal expansion. In general it resembles

somewhat that of the dinosaurs in that it is rodlike rather than platelike. Proximally the ischium bears a large expanded head with a prominent lateral lip. As usual, the anterior portion of the head is considerably thinner than the posterior. Anteriorly, below the lip is a deep concavity, where the bone becomes a thin plate that angles to-

TABLE 4. MEASUREMENTS OF THE HIND LIMB OF *SAUROSUCHUS GALILEI* (IN CENTIMETERS).

|  | PVL 2267 | PVL 2557 |          |
|--|----------|----------|----------|
| <b>Femur</b>   |          |          |          |
| Approximate total length   | 65.0     | —        |          |
| Maximum width of proximal articulation                             | —        | 7.0      |          |
| Distance of 4th trochanter from head                               | 17.0     | 26.0     |          |
| Thickness of shaft at midpoint                                     | 5.0      | —        |          |
| Approximate width of distal articulation                           | 9.0      | —        |          |
| <b>Tibia</b>   |          |          |          |
|  | PVL 2472 | PVL 2267 | PVL 2557 |
| Length   | 46.5     | 45.0     | —        |
| Minimum shaft width  | 4.0      | 3.5      | —        |
| Width distal articulation  | 6.5      | 5.5      | 6.8      |
| Width proximal articulation  | 12.0     | —        | —        |
| <b>Fibula</b>  |          |          |          |
|  | PVL 2267 | PVL 2557 |          |
| Length approximate   | 43.0     | —        |          |
| Minimum shaft width  | 2.7      | 3.0      |          |
| Anteroposterior width of distal articulation                       | 8.5      | 8.2      |          |
| Transverse width of distal articulation                            | 4.0      | 5.3      |          |
| Distance between distal articulation and ilio-fibularis trochanter | 21.0     | 22.0     |          |
| <b>Astragalus</b>  |          |          |          |
|  | PVL 2472 | PVL 2557 |          |
| Maximum width across anterior face                                 | 10.5     | 10.6     |          |
| Maximum anteroposterior length                                     | 8.5      | 9.6      |          |
| Height on anterior face  | 3.8      | 5.0      |          |
| <b>Calcaneum</b>   |          |          |          |
|  | PVL 2267 | PVL 2557 |          |
| Maximum anteroposterior length                                     | 12.5     | 16.0     |          |
| Maximum height of tuber  | 7.5      | 11.0     |          |
| Maximum height of anterior face                                    | 3.8      | 5.5      |          |
| Maximum transverse width   | 8.0      | 8.5      |          |

wards the midline, terminating in a smooth rounded border that does not touch its opposite member. Posterodorsally, the ischium is a heavy rounded strut arising from the thick buttress that forms the posteroventral rim of the acetabulum. Distal to the expanded head region the two ischia are solidly fused. The symphysis forms a slight ridge down the ventral (anterior) surface of the paired bones. At the distal termination the ischium flares out to a moderately expanded foot, similar to that of *Ticinosuchus*, but more rodlike. In cross section the rod portion is tear-drop shaped, the thin portion being fused to its opposite. This fusion created a channel

along the dorsal midline and a corresponding ridge along the ventral surface. The ischium makes an approximately 45-degree angle with the iliac blade, and the strut portion is slightly concave upwards.

*Pubis.* Only the proximal portion of PVL 2557 is known. It shows that the dorsal portion of the articulation with the ilium was a very thick continuation of the anterior border of the ilium beneath the blade. Below this thick rounded border, the pubis thins rapidly, matching the thickness of the ilium. As noted previously, only the edge of the pubis actually participates in the acetabular depression. From the cross section of the broken portion of the





Figure 9. Femur of *Saurosuchus*, composite drawing.  
 $\times \frac{1}{3}$ .

pubis, it would appear that the bone thinned considerably in its anterior portion below the rounded dorsal margin.

*Femur.* The femur is known from two nearly complete specimens. The complete proximal half of the femur is well preserved in specimen PVL 2557, and was found articulated with the corresponding pelvis. It is well-preserved material but appears to be slightly compressed. PVL 2267, the other femur, consists of a complete shaft but lacks the extreme articular surfaces at both ends. This specimen was figured by Reig (1961) and shows a slight intertrochanteric depression. The depression is a deformation of the particular specimen and not a true anatomical feature.

In its overall aspect, the femur of *Saurosuchus* is of the crocodile type rather than like that of the dinosaurs. The proximal portion is a flange with a wedge-shaped articular head. The shaft is gently sigmoid and oval-shaped in cross section. Distally the termination flares out to what must have been large articular condyles. Owing to the deformation of PVL 2267, it is not possible to determine the degree of rotation of the two extremes, but it appears to have been slightly greater than that of crocodiles. The proximal articulation consists of a rugose tear-drop-shaped surface, the broad portion of which forms a continuation of the thick anterior border of the femur. Behind this section the bone thins rapidly to the posterior edge. In PVL 2557 the broad portion is 5.5 cm thick, the tapered posterior edge is 2 cm. Curvature of the head in toward the acetabulum takes the form of an arc along the anterior border and reaches a maximum of 4 cm of inward displacement from the shaft. There is no formation of structures that can be defined as greater or lesser trochanters. The anterior border of the femur is uniformly thick below the articular head, but in the upper portion it thins rapidly, forming a slight depression on the posterior flange area. Ventrally the bone is smooth, decreasing in thickness from the expansion

of these; there is no intertrochanteric fossa. The posterior edge of the flange area thickens rapidly, becoming part of the shaft at the level of the fourth trochanter. Midway between the articular head and the fourth trochanter a slight expansion is present on the posterior edge. The fourth trochanter is a relatively small rugose bulge arising in the center of the ventral surface, approximately one third of the way down from the proximal articulation, very much like that of crocodiles. Below the fourth trochanter, at approximately half the total length, the proximal flattened expansion disappears into the oval-shaped shaft.

Distally the shaft expands evenly into the distal condyles. These are not preserved, but a remnant of the intercondylar fossa on the dorsal surface indicates that the posterior condyle was the larger of the two.

*Tibia.* This bone is known from the complete but poorly-preserved specimens PVL 2472, PVL 2267, and the well-preserved distal half of PVL 2557. The tibia is a robust bone approximately twenty percent shorter than the femur. Proximally, the head expands to a triangular shape, the narrow point of which projects anteriorly and medially to form the cnemial crest. This crest extends down one third of the length before merging with the shaft. Posteriorly, the proximal surface is separated by a prominent depression into the condyles for articulation with the femur. This area of PVL 2472 is shattered, but from the area surrounding the depression it would appear that the two condyles were of nearly the same size. The medial surface of the proximal expansion formed the shortest leg of the triangle and bears a slight depression, probably indicating the contact for the fibula. Anterolaterally a broad flat area was present, separating the cnemial crest from the lateral condyle. The shaft is long, subround in cross section and slightly flattened on the anterolateral surface. Distally, the tibia flares out to a transverse expansion equal in size to the

articulating surface for the femur. However, it should be noted that in actual articulation with the astragalus the tibia was rotated approximately thirty degrees, orienting the cnemial crest directly forward. Thus the lateral side of the distal termination rested on the anterolateral portion of the astragalus and the medial portion on the posteromedial. The lateral expansion is broad and oval-shaped, the medial is narrow and tapering. Separating the two areas of expansion is a narrow groove-like depression on the posterior face that extends up the shaft to the midpoint (see Plate 2). The major surface of articulation is concave on the underside. All articulations are well ossified and have a shiny surface.

*Fibula.* The fibula is known from the right distal half of specimen PVL 2557. The shaft is oval in cross section, the long axis oriented anteroposteriorly, and is flat on the medial surface facing the tibia. The most prominent feature of the shaft is the large tubercle on the anterolateral face, just above the midpoint. Presumably, this was for the insertion of the iliofibularis muscle. Above the tubercle the shaft curves slightly outward; below, it is characteristically concave toward the tibia. Distally the tibia has a flared surface for articulation with the calcaneum and astragalus. The articulating surface is lower on the lateral side than on the medial, and bears two grooves corresponding to the two tarsal elements. Articulation with the calcaneum occurs on the large lateral expansion behind an anterolateral groove of the bone. The astragalus articulation occupied a smaller diagonal groove on the anteromedial side of the distal termination.

*Tarsus.* The tarsus of *Saurosuchus* was of the "crocodilian" type, in which the calcaneum was functionally a part of the foot and the astragalus rotated with the crus. Four elements were present: proximally the large triangular astragalus and the equally large tuberos calcaneum, distally a large lateral tarsal and a much smaller medial one. Elements preserved are: left and right

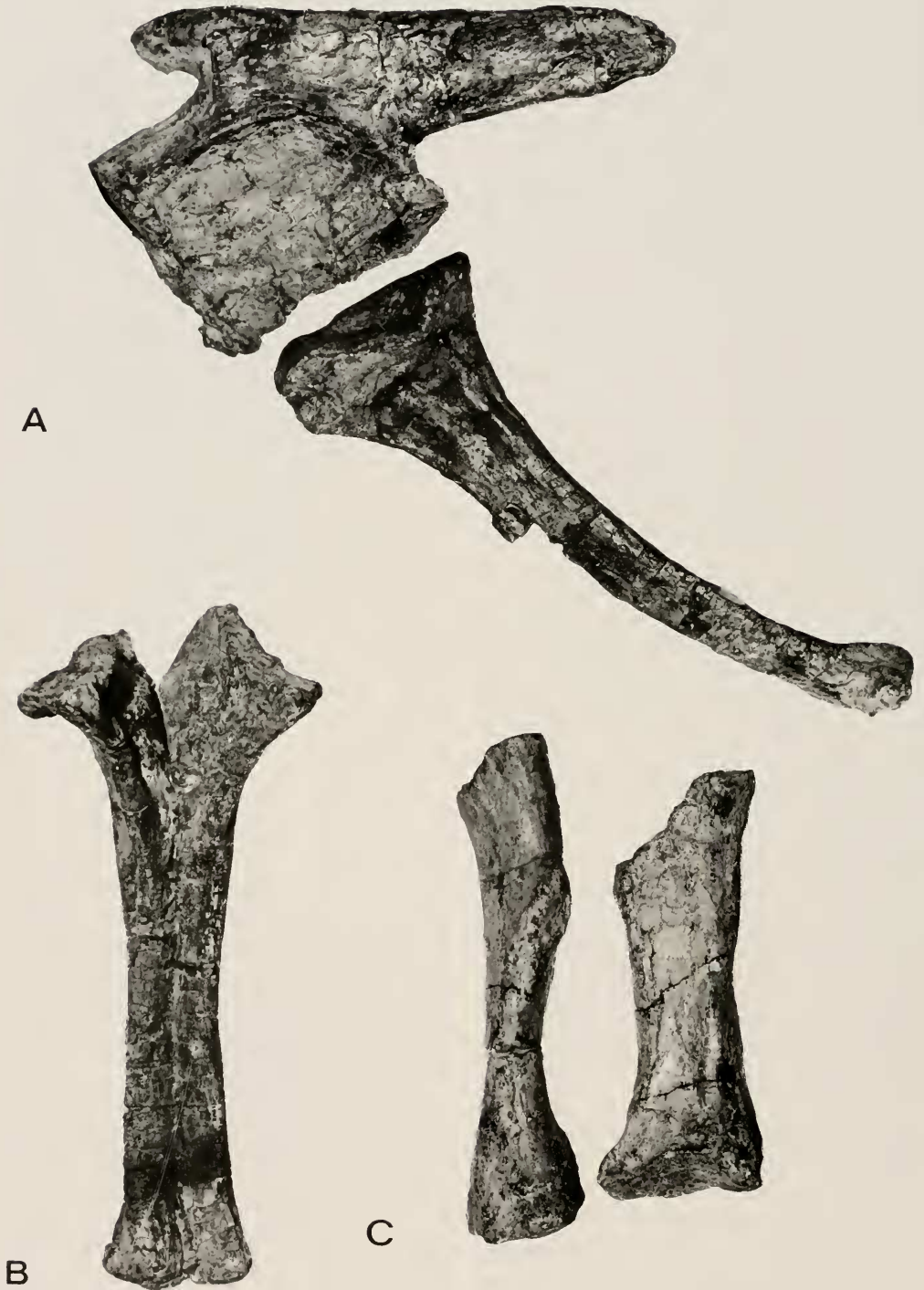


Plate 2. A. Ilium and Ischium of *Saurosuchus*, PVL 2198.  $\times \frac{1}{8}$ . B. Dorsal view of the paired Ischia.  $\times \frac{1}{4}$ . C. Distal portions of the tibia and fibula of *Saurosuchus* specimen, PVL 2557.  $\times \frac{1}{4}$ .



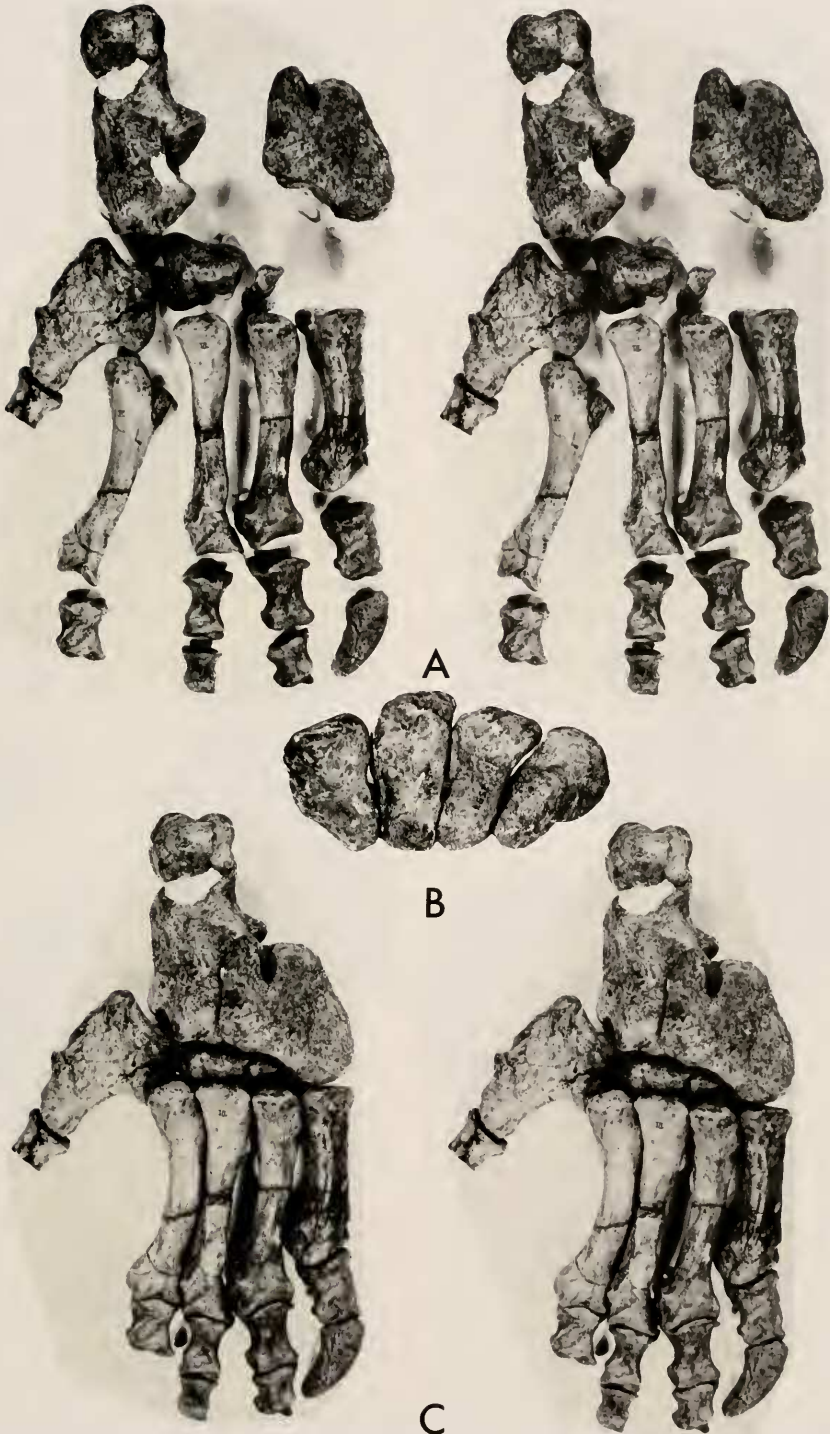


Plate 3. A. Exploded and stereo view of the foot and tarsus, PVL 2557. B. Proximal view of the articulated metatarsals. C. Articulated foot.

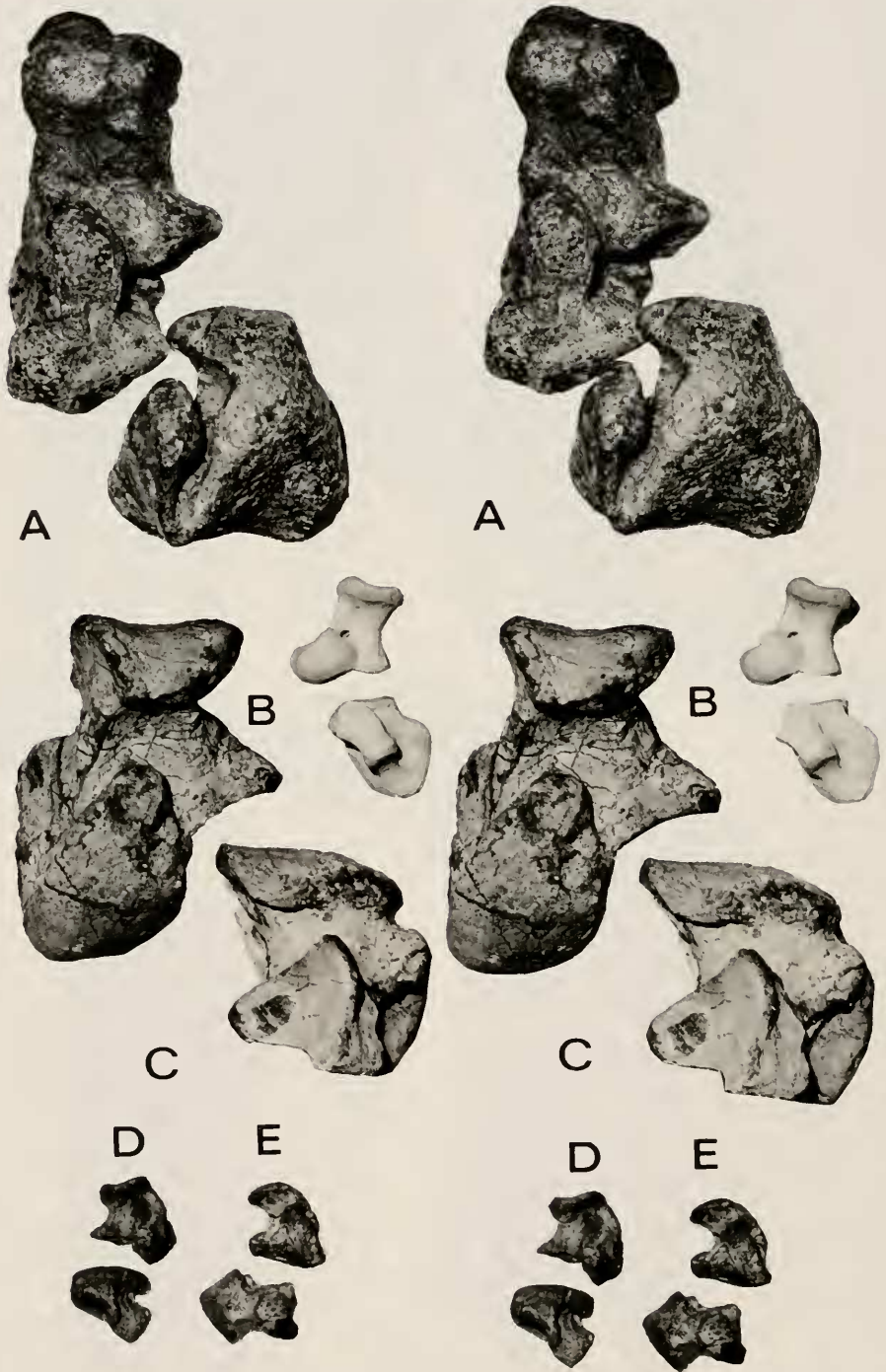


Plate 4. Stereo views of Tarsal elements of: A. *Saurosuchus*, B. *Crocodylus*, C. Undescribed rauisuchid from Los Colorados Fm. (courtesy of Jose Bonaparte), D. *Neoaetosauroides*, E. *Riojasuchus*. (All to same scale.)

calcaneum of PVL 2262, left astragalus of PVL 2472, all poorly preserved but easily identifiable, and the extremely well-preserved complete tarsus and foot of PVL 2557. Adequate description of these complex irregular bones is difficult, and the reader is referred to the stereo-photographs (Plates 3 and 4). The tarsus of *Saurosuchus* appears to be virtually identical to that of *Ticinosuchus*, as described by Krebs (1965), except for minor details. However, *Saurosuchus* was a much larger animal and the tarsal elements are naturally much larger and more heavily constructed. All tarsal elements were well ossified.

*Astragalus*. The astragalus is an irregular triangular block of bone. On its dorso-medial surface it bears a large, triangular, saddle-shaped area for articulation with the tibia. On the lateral side and separated from this area by a small, steep, forward-inclined ridge, lies the much smaller facet for articulation with the fibula. This surface is much more steeply inclined than that of the tibial articulation, and lies at approximately seventy degrees to it. Anteriorly, the surface of the bone bears a deep excavation, common to most reptiles that have a crocodyloid tarsus, medial to which is the bulbous convexity for articulation with the first metatarsal. A notable feature of the astragalus is its shallow depth. Thus the anteriormost border of the tibial facet is practically on the same level as the first metatarsal articulation. Posterolaterally the face of the astragalus is inclined downward from the peak of the ridge separating the epipodial articulations to the rounded ball that articulates with the calcaneum. Just behind the ridge peak a deep groove is present, which opens up posteroventrally to a curved depression in front of the ball joint. This depression fits over the anteromedial rounded border of the calcaneum. When thus articulated the fibular facets of both astragalus and calcaneum are brought together and a more or less double ball and socket joint is formed. The posteromedial border of the

astragalus forms a rather featureless thick rounded border.

*Calcaneum*. Basically, the calcaneum is a rectangular block of bone that bears a posterior upturned tuber and a medial process that forms the rear border of an anteromedially directed hemispherical socket. Four polished articular surfaces are present on the bone. The anteriormost border is formed by the rounded, slightly ginglymoid articular surface for the fibula. This area is clearly marked and by its terminal position indicates that the calcaneum must have been strongly rotated through its transverse axis, elevating the anterior end and depressing the tuber portion. Medial to the fibular facet is the rounded convexity that faces anteromedially at a forty-five degree angle from the face of the fibular surface, which articulated with the previously described concavity of the astragalus. Again, the area of movement is well marked by the polished surface. Immediately behind this area is the small excavation that forms the anterior expression of the hemispherical socket that constitutes the major articulation between the two proximal tarsal elements. This excavation is continued medially onto the anterior face of the medially projecting process mentioned above, the whole forming a well-developed spherical depression directed inward at an angle of approximately forty-five degrees from the anterior face. The fourth articular surface is a small rounded depression ventral to the fibular facet. This was for the reception of the large fourth tarsal bone. On the dorsal surface of the calcaneum, behind the fibular facet and lateral to the socket, lies a raised molding of bone that did not function as an articular surface and is not marked by muscle or tendon scars. It appears to have been an artifact of ossification. Continuing dorsally, the large tuber calcaneum projects upward and rearward. The dorsal and posterior surface of the tuber is rugose, indicating ligament attachment. The lateral surface is a flat wall, slightly depressed in



TABLE 5. MEASUREMENT OF THE PES OF *SAUROSUCHUS GALILEI* (IN CENTIMETERS).

|  |                |                |                 |                 |                  |                  |                 |                |
|--|----------------|----------------|-----------------|-----------------|------------------|------------------|-----------------|----------------|
| Lateral tarsal                                       |                |                |                 |                 |                  |                  |                 |                |
| Transverse width of anterior face                    | 7.0            |                |                 |                 |                  |                  |                 |                |
| Length of lateral articulation with fifth metatarsal | 5.5            |                |                 |                 |                  |                  |                 |                |
| Maximum height                                       | 4.0            |                |                 |                 |                  |                  |                 |                |
| Medial tarsal  |                |                |                 |                 |                  |                  |                 |                |
| Height   | 3.3            |                |                 |                 |                  |                  |                 |                |
| Width  | 2.2            |                |                 |                 |                  |                  |                 |                |
| Metatarsals PVL 2557                                 | I              | II             | III             | IV              | V                |                  |                 |                |
| Length   | 13.7           | 17.2           | 17.7            | 16.5            | 12.0             |                  |                 |                |
| Minimum shaft width                                  | 2.5            | 2.6            | 2.2             | 2.2             | —                |                  |                 |                |
| Width proximal end                                   | 4.0            | 3.5            | 3.9             | 3.9             | 8.0              |                  |                 |                |
| Height proximal end                                  | 6.3            | 7.6            | 7.2             | 7.0             | —                |                  |                 |                |
| Width distal end                                     | 3.5            | 4.5            | 3.8             | 4.0             | 4.0              |                  |                 |                |
| Height distal end                                    | 4.7            | 4.6            | 3.8             | 3.5             | —                |                  |                 |                |
| Phalanges  |                |                |                 |                 |                  |                  |                 |                |
| PVL 2557   | I <sub>1</sub> | I <sub>2</sub> | II <sub>1</sub> | II <sub>2</sub> | III <sub>1</sub> | III <sub>2</sub> | IV <sub>1</sub> | V <sub>1</sub> |
| Length   | 5.6            | 8.5            | 5.8             | 4.0             | 5.8              | 3.4              | 4.3             | 3.7            |
| Height proximal                                      | 4.3            | 3.4            | 4.1             | 2.7             | 3.9              | 2.9              | 3.0             | 3.0            |
| Height distal  | 2.8            | 1.2            | 2.7             | 2.2             | 2.5              | 2.0              | 2.1             | 2.2            |

the center portion. Ventrally the surface is also flat, but a small pitlike depression is present at the base of the tuber.

*Distal tarsals.* Two distal tarsals were present in the foot of *Saurosuchus*, apparently corresponding to numbers III and IV of the primitive reptilian tarsus. The lateral one is the largest of the two and is tetrahedral in shape; the ventral surface is flat, the other three sides form a rounded pyramid dorsally. The dorsal surface is slightly divided into a concavity for reception of an expansion on the astragalus, and a convexity that fits into a shallow pit on the calcaneum ventral to the fibular articulation. Laterally the fourth tarsal bears a large, saddle-shaped, convex, articular surface for the fifth metatarsal. Antero-medially are two convex surfaces, separated by a prominent groove, for articulation of the third and fourth metatarsals. At the extreme medial tip, beside the convexity for the third metatarsal, lies a small concave

facet for reception of the third tarsal bone (see Plate 3). This element is a small rounded bone wedged between the lateral side of the second metatarsal and the astragalus.

*Pes.* The pes of *Saurosuchus* had five sturdily constructed digits in the usual reptilian fashion. Metatarsal V was widely separated from the others, hooked, and bore a broad medial expansion. The remaining four metatarsals were directed straight out from the foot, with a prominent transverse arch in the "instep" region. It is perhaps notable that the expansion of the proximal articulation surfaces of the metacarpals lies in the vertical rather than the horizontal plane (see Plate 3B). Virtually all of the information available comes from the well-preserved right foot of PVL 2557, which is complete except for some of the distal phalanges. Additional elements of the foot are represented by poorly preserved portions of left and right members of PVL 2267. Apparently the phalangeal formula was 2, 3, 4, 5, 3 in the usual primitive fashion. However, the fifth toe may have been reduced to but one or two phalanges. Metatarsal No. 1 is shorter than 2, 3, or 4, is thick bodied, and bears a pulley-shaped distal articulation behind which a prominent diagonal groove traversed the dorsal surface. Proximally, a concave facet is present on the medial side of the articulating surface, the remainder of the surface being smooth. The lateral margin of the proximal tip is vertical, its shape matching the medial border of the second metatarsal, with which it makes a very close fit. The first phalanx is relatively large, almost half the length of the metatarsal, and bears a proximal concavity with a ventrally projecting "heel" for articulation with the rolling surface of the metatarsal. Distally, the joint with the ungual is a shallow ginglymus, narrow at the tip and expanded ventrally. The ungual is a thick-bodied pointed claw, narrow at the top, wider on the bottom, and is half the length of the metatarsal. Largest of the metatarsals

is the second, although numbers 3 and 4 are of similar length. It bears a large narrow proximal articulation, expanded almost exclusively in the vertical plane. On the medial side of the expansion are two facets for the first metatarsal. Laterally, the proximal articulation forms a straight vertical surface with no overlapping contact for the third metatarsal. Midway down the side is a prominent pit, corresponding to a similarly sized notch on the medial side of the adjacent metatarsal. Presumably this formed a channel for nerve and blood supply. The shaft is thickly built, similar to the construction of the first metatarsal, and is concave on the lateral margin but straight on the medial side. Distally the articulation is a large rolling surface with a prominent groove on the ventral border. Just behind the articular surface, on the lateral side, an indentation is present between the flange of the articulation and the body of the shaft. Shape and articulation of metatarsals show that the axis of the transverse "instep" arch ran between the second and third metatarsals. Two phalanges of the second metatarsal are preserved. As might be expected, they are the largest and most heavily constructed of the digits. The first bears a large concave flange proximally, a short shaft, and a distal articulation similar to that of the metatarsal. However, the groove is considerably larger than that of the metatarsal. The second phalanx is subrectangular in shape, and has a smooth concavity proximally and a pulley-shaped articulation distally. Although the ungual is missing, the size and shape of the distal articulation indicates that the claw was approximately the same size as that of the first ungual. Metatarsal number 3 is appreciably more slender than the others and is slightly longer than the second or the fourth. Its proximal expansion is of similar size and shape to that of metatarsal number 2, but whereas that of the second is a straight vertical surface, the third has a diagonal proximal surface with the dorsal portion extended more posteriorly than the

ventral. The medial margin is expanded at the top to form a bulge, with the aforementioned groove lying just below it. Laterally the proximal articulation bears a concavity on the dorsal portion and a small convexity ventrally, corresponding to opposite features on the close-fitting fourth metatarsal. Distally the articular surface of metatarsal number 3 is similar to that of number 2 but smaller. The rounded flange is more expanded on the medial side than on the lateral, and a groove is present behind the flange on the medial side. Only the first two phalanges are preserved; they are virtually identical to those of the second digit, but somewhat more slender. The fourth metatarsal is slightly shorter and more heavily constructed than the third. Its proximal articulation is diagonal in the vertical plane like that of the third, but on the surface itself a prominent excavation is present below the side dorsal border for the reception of the bulge of the fourth tarsal. A major feature of the fourth metatarsal is its bowed shape; it is concave on the lateral side, with the convex medial side fitting closely against the side of metatarsal number 3. This curvature also serves to rotate the plane of the proximal articulation approximately twenty degrees from the vertical, toward the lateral side, from the plane of the distal articulation. On the lateral surface of the shaft in the proximal region anterior to the articular surface is a prominent triangular depression, apparently for muscles and flesh related to the lateral plantar pad of the foot. Distally, the articular surface consists of a pulley-shaped convexity somewhat different from that of the other metatarsals. The groove runs diagonally across the articulation from ventrolateral to dorsomedial. Ventrally, medial to the groove a prominent heel projects downward. Laterally, just behind the articular surface lies an expanded process that continued onto the shaft, making a pronounced curvature of the lateral border of the shaft, and giving the distal articulation the aspect of being offset towards

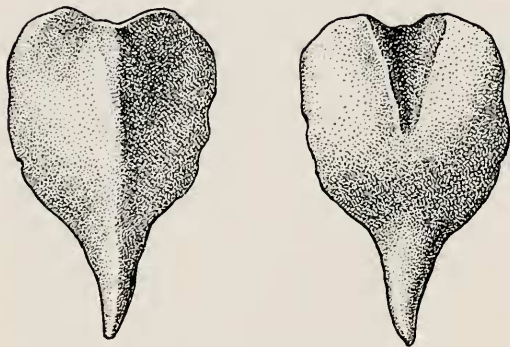


Figure 10. Two views of a posterior scute of *Saurosuchus*. Left, dorsal; right, ventral.  $\times \frac{1}{2}$ .

the medial side (see Plate 3). Only one phalanx of the fourth digit is present; it is rectangular, heavily constructed, and in general similar to that of the second digit, although somewhat smaller and flatter. The proximal surface is more clearly divided into lateral and medial concavities than in the other digits. Distally the articular surface is considerably flatter, and lacks the downward extension of the rolling surface found on the first phalanges of the other digits. These are indications that the fourth toe was probably long and relatively slender. Specimen PVL 2267 has three isolated articulated phalanges that probably belonged to the fourth digit. These show a rectangular shape that rapidly diminishes in length distally with the last of the series, probably the pre-ungual, little more than a transverse rectangular chip of bone. However, the association of these three phalanges (PVL 2267) is not certain. In *Ticinosuchus* all of the phalanges are longitudinally rectangular, as are all of the proximal ones preserved in PVL 2557. Metatarsal number five is a massive hook-shaped element that bears a large hemicylindrical articular surface on its medial side for the matching concavity of the fourth tarsal bone. On the anterodorsal face of the surface is a small facet for the lateral edge of the fourth metatarsal. Behind the large ball surface, the posterior border curves laterally and posteriorly to

terminate in a rounded point at the rear lateral edge. From this point the lateral margin curves out and forward to the distal tip. A small expanded process is present on the lateral edge one third of the way back from the distal articulation. The medial surface of the "shaft" curves smoothly from the anterior tip of the major proximal articulation to terminate in the blunt surface of the distal articulation. This articular surface bears neither flanges nor grooves, but is a simple, slightly convex surface. The first phalanx is rectangular in shape, broader at the proximal end, and bears an expanded concave articular surface that partially envelopes the convexity of the metatarsal. Distally, the phalanx terminates in a simple flat vertical surface devoid of rounded features. No other phalanges are known for the fifth digit. The fifth toe was widely separated from the other digits.

#### DERMAL ARMOUR

Scutes have been found associated only with PVL 2198. These were found partially articulated with the vertebral column, and like most of the vertebrae, are poorly preserved. Three articulated scutes, much smaller than the others, were found in association with the other bones of the specimen, but not in a definable position. As they are very well preserved, and in general the degree of preservation becomes better caudally in PVL 2198, it is assumed that these scutes were from the posterior dorsal region. Two paramedian rows of scutes were present on the dorsal region of *Saurosuchus*, the total width being 10 cm on specimen PVL 2198. As preserved, the two rows do not appear to have been joined by a strong sutural contact. The dorsal scutes are slightly asymmetrical and leaf-shaped in outline, drawn to a point in front and truncated at the rear. They are imbricated, the wide rear margin overlapping the point of the scute just caudal to it. Although the two rows join at the midline, the medial border is only slightly thicker than the



lateral. The anterior point is slightly asymmetrical; it is off center toward the medial border. Dorsally the scutes are gently arched in cross section, slightly more so on the lateral side than on the medial. A keel as such is not present, but there is a slight longitudinal ridge. Possibly a small indentation was present on the posterior border. Ventrally there appears to be but a slight indentation in the posterior portion to receive the point of the following scute. A significant change in size takes place along the length of the series; the posterior scutes are smaller than the anterior ones, changing from approximately 5 cm in width to 4.

The three isolated scutes differ considerably from the others, but are of the same pattern and certainly belong to the same specimen. They are, however, perfectly symmetrical, with each edge tapered to a very thin border (see Fig. 10). Anteriorly the point is longer and more tapered than in the other scutes, and fits into a wedge-shaped groove in the preceding scute. The dorsal surface is prominently ridged in the center, leading to the point anteriorly and to an indentation posteriorly. These characteristics suggest that these were members of a single row of scutes, rather than paired. A similar condition is reported for *Ticinosuchus* by Krebs (1965), and is to be expected given the other similarities of the two genera. The greatest difference between the dorsal and the lumbar scutes is size; the former are 5 cm wide and approximately 7 cm long while the latter are 3 cm wide and approximately 4 cm long. This condition differs from that of *Ticinosuchus* in which the scutes of the unpaired row are larger than the paired. However, the overall aspect of the armour of *Saurosuchus* is that it is more reduced relative to the size of the animal than is that of *Ticinosuchus*.

## DISCUSSION

### Origin of the Rauisuchidae

The anatomical characteristics of the known members of the family strongly

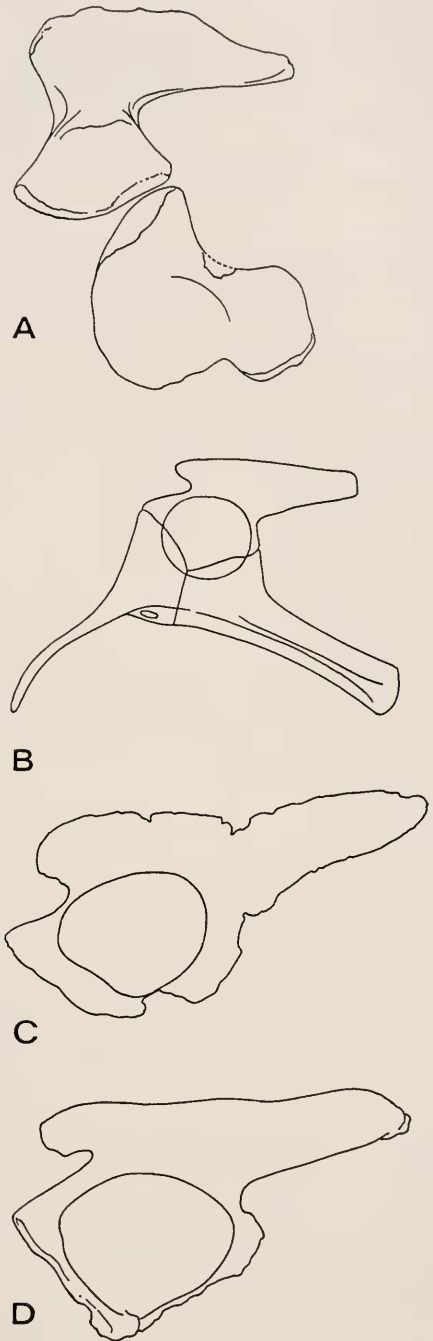


Figure 11. Pelvis of: A, *Shansisuchus* (after Young); B, *Ticinosuchus* (after Krebs); C, *Rauisuchus* (from a photograph in Huene, 1942); D, *Saurosuchus*.

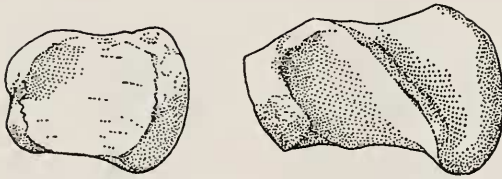


Figure 12. Left, calcaneum; right, astragalus of *Shansisuchus* (after Young).

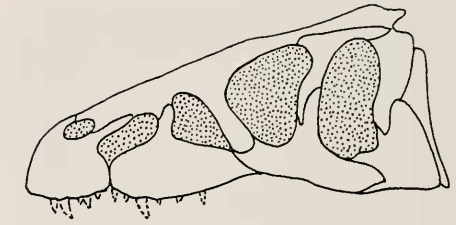
suggest direct derivation from the erythrosuchids, rather than from ornithosuchids or from a common erythrosuchid-ornithosuchid ancestry. Cranial anatomy is but little modified from the erythrosuchid condition (see Fig. 13). Within the Erythrosuchidae, the most advanced member (both anatomically and stratigraphically) appears to be *Shansisuchus* from the Ehrmayng Series of China (see Young, 1964; Reig, 1970; and Charig and Reig, 1970). This genus provides a rather good intermediate between the two families, and indeed was tentatively included in the "Prestosuchidae" by Romer (1972a). However, it still retains the primitive pelvic girdle and simple tarsal structure common to the Erythrosuchidae. As locomotory abilities seem to have been a principal evolutionary factor within the Rausuchidae, it would seem appropriate to consider the less advanced *Shansisuchus* as an erythrosuchid.

Major characteristics of the rausuchids that can be traced with a reasonable degree of confidence through the lineage are:

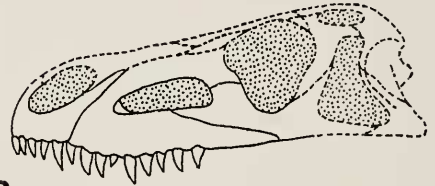
1) Skull configuration: a keyhole-shaped orbit, large antorbital fenestra surrounded by a smooth depression, small supra-temporal fenestra, high narrow cranial table, and a posterior prong on the premaxilla. Some of the genera have an accessory antorbital fenestra between the premaxilla and the maxilla.

2) Vertebrae: high neural arch, straight rectangular spine with distal expansion, deep interspinous clefts.

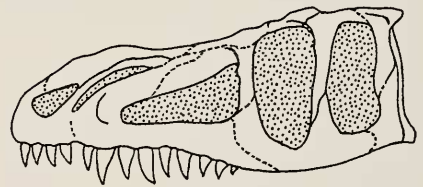
3) Pelvis: prominent posterior spine, presence of a brevis shelf, styliform ischium with an expanded tip, greatly reduced pubic plate, pubis with slight participation in the acetabulum.



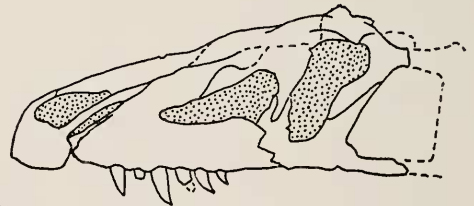
A



B



C



D

Figure 13. Comparison of cranial morphology in A, *Shansisuchus* (after Young); B, *Ticinosuchus* (modified from Krebs); C, *Luperosuchus* (from Romer); D, *Saurosuchus*. Not to same scale.

4) Femur: crocodilelike, without rounded medial expansion.

5) Tarsus: ball and socket crocoid type, fifth metatarsal hooked.

The several genera that make up the

Rauisuchidae can be separated into three morphologic groupings that reflect both their stratigraphic position and their probable phylogeny: 1) an early group, represented by *Ticinosuchus* from the earliest Middle Triassic; 2) an extensive intermediate group represented by *Luperosuchus*, *Stagonosuchus*, "*Mandasuchus*", *Prestosuchus*, and *Rauisuchus* from the later Middle Triassic; and 3) *Saurosuchus* and the undescribed form from the Los Colorados, of earlier and later Late Triassic respectively. *Ticinosuchus*, the earliest member of the family, and the only one known from a complete skeleton, has a skull that has been highly fractured and compressed to a largely two-dimensional state. As reconstructed by Krebs, the skull is similar, but not strikingly so, to *Saurosuchus* and *Luperosuchus*. However, using the more complete knowledge afforded by the Argentine specimens, it is possible to reinterpret to some degree the skull of *Ticinosuchus* on the basis of the published photographs. Two modifications of Krebs' reconstruction appear feasible: the antorbital fenestra was probably smaller than shown and was surrounded by a smooth shelf, and the anterior border of the maxilla was inflected just above the tooth row, possibly indicating a small accessory opening similar to that of *Saurosuchus*.

Cervical vertebrae represent the only anatomical character that shows a considerable degree of variation among the several genera of the family. In *Ticinosuchus* the cervicals are elongated, but otherwise unspecialized. A similar condition appears to be present in "*Mandasuchus*" but not in *Stagonosuchus*, *Prestosuchus*, or *Rauisuchus*. Only one cervical vertebrae is known from *Saurosuchus*; it is a highly specialized elongate structure so different from other known forms that it is assigned to the genus with reservation.

In the other comparable features characteristic of the family, there is a remarkable similarity among the genera definitely assigned. More subtle differences dis-

tinguish *Saurosuchus* as the most progressive of the described rauisuchids<sup>1</sup>; centra of the vertebrae are constricted, the ischium is longer and more rodlike, and the femur is more gracile than the corresponding features of the other genera.

Within the Ischigualasto Basin three rauisuchids are found in the sequential continental sediments. The earliest of these is *Luperosuchus* from the Chanares Formation (Romer, 1971a). It has already attained the large size characteristic of most of the family, but is known only from an incomplete skull. Changes in the skull from *Luperosuchus* to *Saurosuchus* to the Los Colorados form were slight; the orbit became more circular in the upper portion and the smooth shelf around the antorbital fenestra is larger in the later genera. It seems reasonable to assume that these three forms were continuous members of a single regional lineage. Very possibly *Prestosuchus* from Brazil should be included in the lineage. *Prestosuchus* is very comparable to *Saurosuchus*; apparently the only significant difference is that the femur of the former appears to be more heavily constricted and less gracile than that of the latter. Relationship of the Ischigualasto Basin forms to other members of the family is not as close. The vertebrae of *Stagonosuchus* are somewhat constricted like those of *Saurosuchus*, but the pelvis is more primitive. "*Mandasuchus*" is quite similar to *Saurosuchus*, and the two may be congeneric or they may be closely related forms similar to *Prestosuchus* and *Rauisuchus*. *Rauisuchus* itself is less like the other members of the family and its association with the group has been questioned (Charig 1967, Romer, 1972a, Walker, personal communication). Walker (personal communication) has suggested that *Rauisuchus* may be an ornithosuchid. His suggestion is based principally on some aspects

<sup>1</sup>The undescribed rauisuchid from the Los Colorados Formation is larger than *Saurosuchus*; it had a considerably more advanced tarsus, but a very similar skull (Bonaparte, personal communication).



of the skull fragments and on the dermal armour. However, the premaxilla bears the posterior projecting prong that separates the external naris from the maxilla, and its overall shape is similar to that of *Saurosuchus* and *Luperosuchus*. The ilium figured by Huene (1942, plate 27) is remarkably like that of *Prestosuchus* and *Saurosuchus* (see Fig. 7). Other elements are not as closely comparable, giving rise to the doubts about the affinities of the genus. However, the morphology of the vertebrae and dermal armour are not inconsistent with that of the other members assigned to the family, and their resemblance to ornithosuchids may be superficial, as are a number of the resemblances between the two groups (see discussion of vertebrae and tarsus). For the present, I would leave *Rauisuchus* in the family association that is termed "Prestosuchidae" by some authors, but recognize that it is less comparable to the larger genera *Prestosuchus*, *Saurosuchus*, and "*Mandasuchus*" than these are to each other.

It would seem likely then that the Brazilian and Argentine genera were part of a South American radiation, perhaps from a *Luperosuchus*-like stock. The African forms, *Mandasuchus* and *Stagonosuchus*, may represent a separate but closely related line.

A summary of the evolutionary history of the Rauisuchidae would then be: origin in the early Middle Triassic from a progressive group of erythrosuchids, the first members of the family probably near the *Ticinosuchus* level; adaptive radiation in the Ladinian and Carnian; survival of specialized members that could compete with dinosaurs in the uppermost Triassic, and extinction of the group by the Early Jurassic (see Fig. 14).

### Habits of the Rauisuchidae

On the basis of the known remains, the rauisuchids can be described as large quadrupedal animals ranging in total length from three to six meters. The sharp

serrated dentition leaves no doubt that they were carnivores, and the deep narrow skull would suggest predaceous habits. During the Middle and Late Triassic they were probably among the largest of the terrestrial carnivores. Regarding locomotion, the hind limbs were of the crocodyloid grade of evolution, and as such the rauisuchids were reasonably good runners, although no doubt less agile than the later dinosaurs and probably less agile than the contemporary Ornithosuchidae.<sup>1</sup> Rise of the rauisuchids may have been parallel to the rise of the rynchosaurs and the gomphodont cynodonts during the Ladinian and Carnian in a predator-prey relationship. It is usually assumed that the large thecodont predators disappeared during the Late Triassic owing to the competition from dinosaurs. However, the presence of a very large, advanced rauisuchid in sediments considered to be Late Norian in age (see Bonaparte, 1972a and Sill, 1969 for details on the stratigraphic relationships of the Argentine Triassic), would indicate that these thecodonts had become adapted to prey on the early saurischians, many of which were herbivores. The last known rauisuchid was a very large animal and had an advanced digitigrade foot. Nevertheless, the femur remained at the crocodyloid stage of development, namely, without the formation of a medial condyle or a shift to the parasagittal plane of the body. Assuming that the vertical position of the limbs was an important adaptation, the rauisuchids would have been at a disadvantage with regard to the emerging carnivorous dinosaurs. Such a relationship presumably would explain the extinction of the group as the dinosaurs became dominant.

### Thecodont Taxonomy and Phylogeny

Although thecodonts have long been recognized as the key group in the rise of

<sup>1</sup> However, Bakker (1972, and in press) has shown by experimental data that the physiologic cost of locomotion is dependent only on speed and body weight, entirely independently of limb posture.

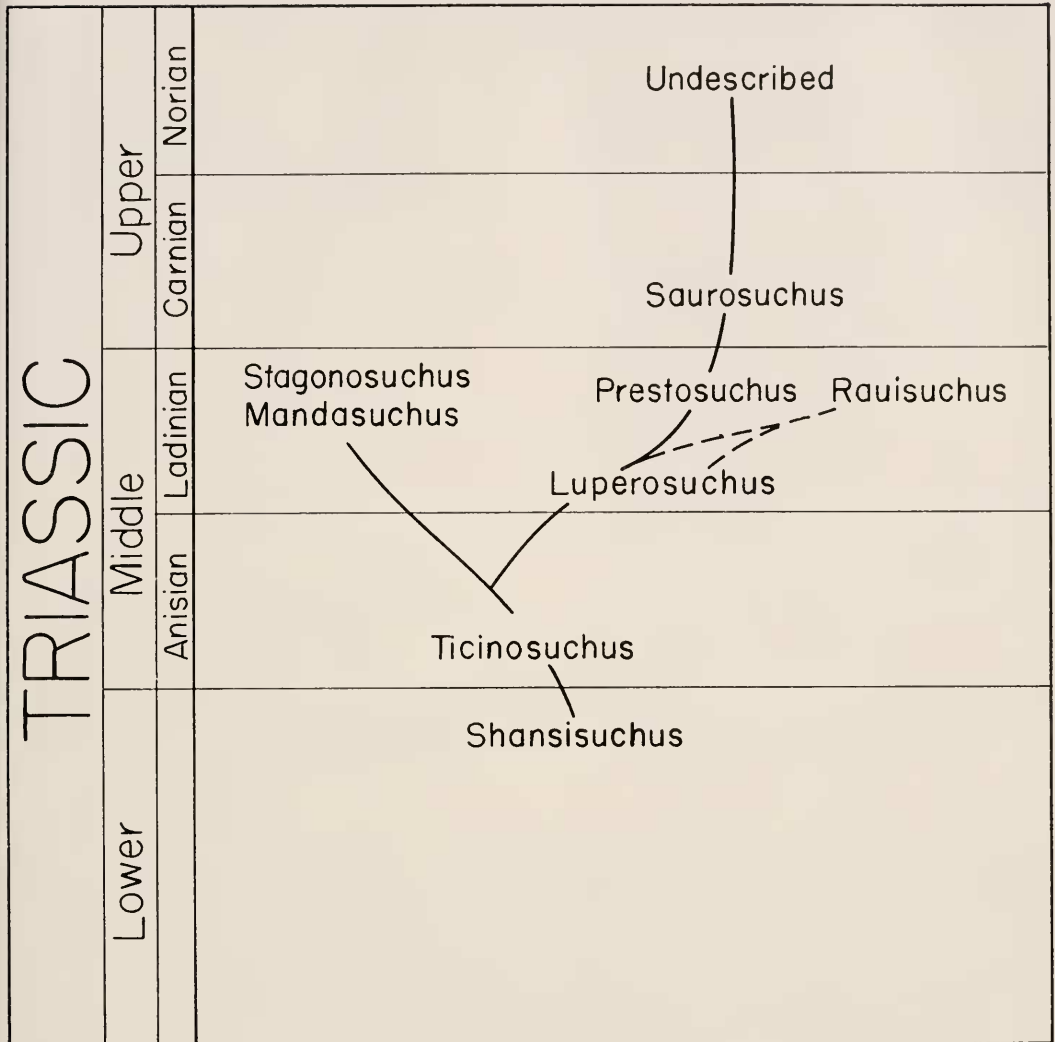


Figure 14. Suggested phylogeny of the Rauisuchidae.

the archosaur faunas that dominated the later Mesozoic, they have been a poorly known and confusing group. As new discoveries have been made in the last few years there has been a renewed interest in the order, and at last the prospect emerges of unraveling the many and varied thecodont lineages. Traditionally, thecodonts have been divided into three groups: 1) the very primitive forms from the Early Tri-

assic, 2) the highly specialized taxa of the Late Triassic, phytosaurs and aetosaurs, and 3) the main stream, Pseudosuchia, somewhat of an "everything else" suborder. The new discoveries have permitted the clarification of some relationships, and have added a new lineage, Proterochampsididae, to the order. But the major relationships are still far from settled, and there is a considerable number of genera that do

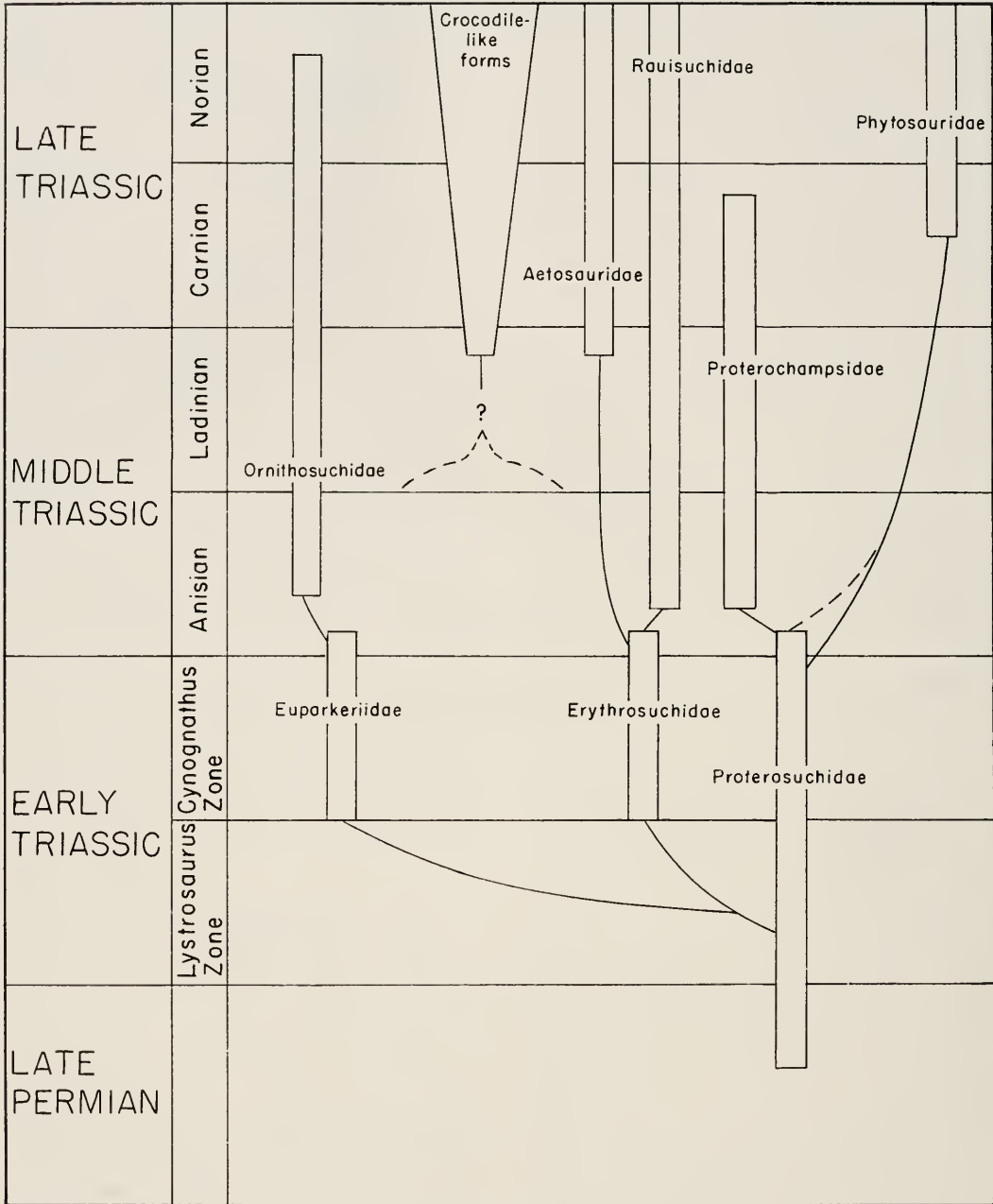


Figure 15. Suggested phylogeny of some thecodont lineages.

not fit into known families or even sub-orders.

Current thinking on thecodont taxonomy is perhaps best reflected in recent papers

by Romer (1972a) and by Bonaparte (1971), as follows (the sequential order followed by these authors has been changed to facilitate comparison):



| Romer                                 | Bonaparte                               |
|---------------------------------------|---|
| Order Thecodontia                     | Order Thecodontia                       |
| Suborder Proterosuchia                | Suborder Proterosuchia                  |
| Family Proterosuchidae                | Family Proterosuchidae                  |
| Family Erythrosuchidae                | Family Erythrosuchidae                  |
| Family Prestosuchidae (=Rauisuchidae) |   |
| Family Proterochampsidae              |   |
| Suborder Pseudosuchia <sup>1</sup>    | Suborder Pseudosuchia                   |
| Family Ornithosuchidae                | Infraorder Ornithosuchia                |
|                                       | Family Ornithosuchidae                  |
|                                       | Family Rauisuchidae                     |
|                                       | Family Pallisteridae                    |
|                                       | Family Teleocrateridae(?)               |
| Family Scleromochlidae                | Family Scleromochlidae                  |
|                                       | Infraorder Sphenosuchia                 |
|                                       | Family Sphenosuchidae                   |
|                                       | Family Triassolestidae                  |
|                                       | Infraorder Proterochampsia <sup>2</sup> |
|                                       | Family Cerritosauridae                  |
|                                       | Family Proterochampsidae                |
| Suborder Aetosauria                   | Suborder Aetosauria                     |
| Family Aetosauridae (=Stagonolepidae) | Family Stagonolepidae (=Aetosauridae)   |
| Suborder Parasuchia (Phytosauria)     | Suborder Parasuchia                     |
| Family Phytosauridae                  | Family Phytosauridae                    |

<sup>1</sup> The family Sphenosuchidae was placed by Romer in the suborder Proterosuchia of the Crocodilia. *Teleocrater* and *Triassolestes*, together with other poorly known genera, are not assigned to families.

<sup>2</sup> The suborder Archeosuchia was previously erected for the Proterochampsidae (Sill, 1967).

Both of these authors retain the usual categories mentioned previously, but it is interesting to note the different interpretations given to the newly defined lineages Rauisuchidae and Proterochampsidae. Romer considers them to be continuations of the primitive radiation, while Bonaparte would suggest they are offshoots of the pseudosuchian stock.

It is perhaps still premature to restructure thecodont taxonomy, but the new discoveries do make it possible for the first time to trace some of the lineages throughout the Triassic.

Primitive thecodonts consist of three families; the ancestral stem Proterosuchidae (see Cruickshank, 1972), the large terrestrial Erythrosuchidae, derived from the Proterosuchidae, and the progressive Euparkeriidae, usually considered the first of the Pseudosuchia (see Ewer, 1965 and Charig

and Reig, 1970). The proterosuchids were probably aquatic or semi-aquatic carnivores that somewhat resembled crocodiles. Erythrosuchids show many characters that relate them to the stem group, but were fairly large terrestrial carnivores. *Euparkeria* was apparently derived from an early lineage that separated from the Erythrosuchidae and evolved rapidly towards a more agile locomotory system. It has usually been assumed that it was the euparkeriid stock that produced the later thecodont radiation (Romer, 1966, and other textbooks). The new discoveries of fossil thecodonts, in particular those from South America, make it possible to connect some evolutionary lines of all three primitive groups from the Early to the Late Triassic.

As has been noted previously, the origin of the Rauisuchidae almost certainly lies in the Erythrosuchidae. Rauisuchids can be

traced through much of the Triassic with closely related forms present in every stage of the period from the Anisian to the Norian (see Fig. 14). The Proterochampsidae represents a newly defined lineage at present known only from South America. Earliest members of the family are from the Chañares Formation, *Chanaresuchus* and *Gualosuchus*, probably of Early Ladinian or Late Anisian age (Romer 1971b). Later forms occur in the Santa Maria Formation of Brazil, *Cerritosaurus* (Price, 1946; Bonaparte, 1971), and in the Ischigualasto Formation of Argentina, *Proterochampsia* (Reig, 1959; Sill, 1967). Most members of the family show semiaquatic tendencies, the Brazilian form *Cerritosaurus* less so, and *Proterochampsia* itself more so. The apparently more aquatic habitus of *Proterochampsia* was used by Bonaparte to separate the other genera from it as the family Cerritosauridae, but the genera are no doubt closely related and probably should be placed in the same family. Placing the Proterochampsidae as an infraorder of the Pseudosuchia implies a common origin after the acquisition of the pseudosuchian adaptive characteristics. It appears more likely that the Proterochampsidae were independent derivatives of the primitive stem proterosuchians, as suggested by Romer's classification, but they had advanced beyond the level common to the proterosuchids and erythrosuchids. On the basis of the skull, I previously (Sill, 1967) believed them to be primitive crocodiles, but the postcranial material of the earlier forms described by Romer renders this interpretation unlikely.

The third lineage to be well documented is not new at all, but is the "mainline" family Ornithosuchidae. As redefined by Bonaparte (1972a) this family would be restricted to the following well-defined genera: *Venaticosuchus* from the Ischigualasto Formation (Bonaparte, 1972b), *Riojasuchus* from the Los Colorados Formation (Bonaparte, 1969, 1972a), and *Ornithosuchus* itself from the Elgin Sand-

stones (Newton, 1894; Walker, 1964). To these Romer (1972b) recently added *Gracilisuchus* from the Chañares Formation. These genera in turn show reasonably close affinities to *Euparkeria*, and appear to represent a descendant lineage from the euparkeriid type of early thecodont.

In tracing these families from their origins in the early history of the Thecodontia, mention has been made only of those genera that are well enough known to show definite relationships; there are, of course, still many thecodonts whose systematic associations are not clear at present and who are usually assigned to families on a rather uncritical basis.

There remains the two well-known specialized suborders, the Aetosauria and the phytosaurs. In general these groups are limited to the Late Triassic, although an isolated phytosaur has long been noted, and disputed, from the Early Triassic of Europe (Jackel, 1910; Gregory, 1962). Phytosaurs are well known morphologically, except for the tarsus, but no sure indication exists regarding their relationship to the primitive groups. In general it has been assumed that they were precrocodylian derivatives of the Pseudosuchia, driven into extinction by the appearance of the true crocodiles (see Gregory, 1962). However, phytosaurs were basically primitive animals, retaining additional skull elements that were lost early in the development of the other thecodonts. Also, the pelvic girdle consisted of large platelike bones similar to the pattern of the primitive groups (see Camp, 1930; Gregory, 1962, 1969). On the basis of the recently described proterochampsids, it seems possible that phytosaurs may have been derived from an earlier continuation of the aquatic forms of the Proterosuchia.

Aetosauroids are the other closely-knit group of specialized thecodonts. Like phytosaurs they are known principally from the Upper Triassic, the earliest ones coming from the Ischigualasto Formation of Argentina (Car-

nian).<sup>1</sup> Those from Ischigualasto are fully specialized members of the family, bearing little indication of primitiveness. Aetosaurus were probably an early specialization for a rooting, pig-like habit (see Walker, 1961). Aside from their obvious specializations, aetosaurus retain many primitive characteristics common to the Erythrosuchidae and Euparkeriidae. As noted by Ewer (1965), *Euparkeria* was already more advanced in its locomotory apparatus than the aetosaurus. Therefore, the origins of the Aetosauria must have been from a progressive line of erythrosuchids or an early member of the Euparkeriidae. If it is true that the *Euparkeria* lineage represents an early departure from the Erythrosuchidae, based largely on limb specialization, then it would be more likely that the aetosaurus were an independent derivation from the erythrosuchid stem, perhaps from the same group that produced the raiusuchids.

Indirect anatomical evidence supporting the affinity of Aetosauria with erythrosuchids is found in the tarsus. It has long been noted that the astragalus and calcaneum of aetosaurus is of the "crocodile-type" in common with a number of other thecodonts. The closest comparison of these elements seems to be with the Raiusuchidae (see Plate 4).

Another group of thecodonts, which has long been particularly difficult to interpret consists of those that share a number of characteristics of the crocodiles, but are not true crocodiles. These have been an enigma since they were first discovered around the turn of the century. They have been considered alternately as stages in the evolution of crocodiles (Huene, 1925), independent lineages (Haughton, 1924) and aberrant or primitive members of the Crocodylia (Sill, 1967; Romer, 1972a).

Walker (1970) has recently separated out the crocodilelike thecodonts and placed them as a suborder, Paracrocodylia, of equal rank with the Crocodylia in a new order Crocodylomorpha. Walker's work, based largely on re-examination of *Sphenosuchus* and *Hallopus*, indicates the presence of a possibly unified lineage that shared many anatomical characteristics of crocodiles, but were not ancestral to them. Whether or not a new order should be erected to place this group in juxtaposition with the Crocodylia will be decided by future discoveries. At the moment it does not seem to be justified. The Crocodylia are a well-defined group. Walker's Paracrocodylia is based on the Triassic family Pedeticosauridae (or Sphenosuchidae), the genus *Hallopus*—an apparent Jurassic derivative of the earlier family—and the Baurusuchidae, which he removes from the crocodylian suborder Sebecosuchia. Such a classification does not reflect the same degree of natural grouping that is found in the present category Crocodylia. It would seem more reasonable at present to consider the Pedeticosauridae as either a derivation of the thecodont line that gave rise to the true crocodiles, or as aberrant crocodiles from the early radiation of the Crocodylia.

An alternative possibility is that crocodiles arose from an early branch of the Ornithosuchidae, possibly a derivative of the *Euparkeria* line, or from a continuation of the Erythrosuchidae, perhaps from the same stock that produced the Raiusuchidae (and possibly aetosaurus). Evidence suggesting the possibility of such a relationship is found in the similarity of the crocodylian tarsus to that of thecodonts in the above-mentioned categories. The so-called crocodylian tarsal joint, in which the calcaneum bears a prominent tuber and is functionally part of the foot while the astragalus is fixed to the crus, appears to have been better developed in these lines than in either *Proterosuchus* or the Proterochampsidae. In addition, there appears to be a funda-

<sup>1</sup> It is possible that an aetosaurus was present in the earlier Ehrmayng Series of China. A calcaneum figured by Young (1964:81) is very much like that of the Ischigualasto aetosaurus, and quite unlike that of ornithosuchians.



mental difference between the construction of the tarsus in ornithosuchids and the groups presumably derived from erythrosuchids. In the Ornithosuchidae the major joint between the proximal tarsal elements is formed by a ball on the anteromedial surface of the calcaneum and a corresponding socket on the astragalus. On the other hand, in rauisuchids, aetosaurs, and crocodiles, the main socket is on the calcaneum and the ball is on the astragalus. Both forms appear to be functionally the same, but possibly represent parallel evolutionary paths. Recognition of this condition, first noticed by Bonaparte (1971), tends to diminish the difficulty noted by Krebs (1963) and Reig (1970) of explaining apparently unrelated thecodonts that possess very similar complicated tarsal joints. The "true" crocodile tarsus then becomes an impressive argument against derivation of this group from the Ornithosuchidae-Euparkeriidae type of pseudosuchian, and would tend to suggest a closer affinity with the erythrosuchid lineage, and the presumed derivatives of that line. Nevertheless, not enough is known about the tarsal joint of the Proterosuchidae, Proterochampsia, or Phytosauridae, to exclude them from a common ancestry with the Crocodylia. Tarsal joints of various members of the Thecodontia are currently under study by a number of paleontologists, some of whom feel that the structure may represent a key to both thecodont and dinosaur phylogeny.

There remains a considerable number of thecodonts that are not members of any of the groups mentioned in this paper. Some of these are almost certainly cladogenetic derivatives of these groups (see the generic list in Romer, 1966, 1972a). The various phylogenetic possibilities of these forms have been discussed recently by Reig (1970) and little more can be said until additional fossil material is available. In addition there are a number of "ghost thecodonts," forms that have been named and placed in the ordinal hierarchy, but

have never been duly described.<sup>1</sup> These forms, largely from critical Middle Triassic strata, should provide additional insights into the thecodont radiation.

Dinosaur origins remain unclear. Both saurischian and ornithischian representatives are present and clearly recognizable in the Ischigualasto Formation of Argentina (Late Ladinian-Early Carnian); saurischians occur in the earlier Santa Maria Formation of Brazil. There is no solid evidence for linking saurischians with either ornithosuchid or rauisuchid thecodonts. However, Charig (1967) suggested the possibility of prosauropods arising from the latter group (Prestosuchidae in his usage). Reig (1970) considered it more likely that saurischians had descended directly from an erythrosuchid lineage than from a *Euparkeria* type of thecodont. No clues at all exist regarding the origin of the ornithischian dinosaurs; the earliest representative (*Pisanosaurus* from the Ischigualasto Formation) is a fully developed member of the group. It seems to be an inescapable conclusion that dinosaurs separated from thecodonts earlier than has usually been assumed, and that most thecodonts were competitors of dinosaurs rather than their progenitors.

### Thecodont-Dinosaur Transition

It is perhaps paradoxical that the more we learn about thecodont evolution the less we know about dinosaur origins. Theco-

<sup>1</sup> *Mandasuchus* and *Teleocrater* were described by Charig in his doctoral thesis of 1956 and the names then published in an abstract in 1957. The names were incorporated into the literature by Huene (1956) and Romer (1966), but no formal descriptions have ever been published. In a later paper Charig, Attridge, and Crompton (1965) referred to the genera, but added a footnote to the effect that they were *nomina nuda*. Charig (1967) mentions both genera, an additional one from the same area, *Pallisteria*, and also two families, *Pallisteriidae* and *Teleocrateridae*. As author of all three genera and both families, he cites Charig (1967), a paper which has not yet been published. All of these names, except *Pallisteria* and its family, are listed in Romer (1966), but all appear to be without proper foundation.

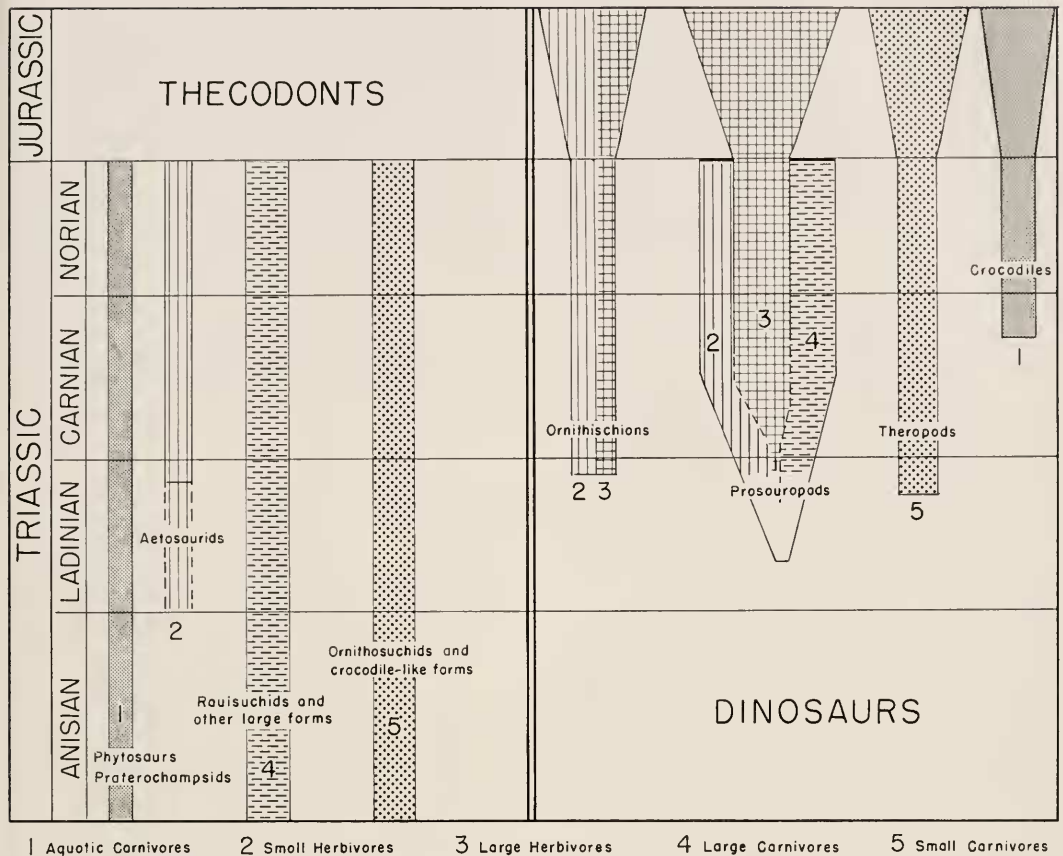


Figure 16. Time-habitat relationships of thecodonts and dinosaurs (see text).

donts evidently were successful, widespread, and diversified during the major part of Triassic time. Yet dinosaurs, usually considered as more or less the end result of thecodont evolution, had their origins well into the Middle Triassic (see Fig. 16). Thecodonts and dinosaurs apparently lived side by side during at least the last half of the Triassic. This situation naturally raises some questions about the selective forces involved and the nature of the competition that presumably existed between the two groups.

The superiority of dinosaurs relative to thecodonts is usually ascribed to a shift from a semi-erect to a fully erect body stance (Bakker, 1971; Charig, 1972). In

this case the more agile dinosaur locomotion supposedly would have driven the thecodonts into extinction (but see footnote, p. 352). However, an early or transitional stage of dinosaurian limb posture is not found in any of the known thecodonts, and in particular there is no evidence of the shift to the simple hinge type of foot characteristic of dinosaurs. Charig (1972) postulated an as yet unknown thecodont ancestor in which the calcaneum was reduced and rotated with the crus rather than with the pes. Reig (1970), on the other hand, would have the dinosaurs originate directly from a primitive thecodont of an erythrosuchid level in the Early Triassic, and evolve essentially independently of the

major thecodont radiation of the Middle and early Late Triassic. However, if this were the case it would be expected that dinosaurs rather than thecodonts would have dominated the Middle Triassic.

The earliest dinosaur remains currently known come from the Manda and Santa Maria Formations of approximately Anisian or Ladinian age (Charig, 1967; Colbert, 1970). These genera, "*Nyasasaurus*" (undescribed) and *Staurikosaurus* are contemporaries of rauisuchid thecodonts, found in the same sediments ("*Mandasuchus*" and *Prestosuchus*). *Staurikosaurus* was more over a predator of approximately the same size as *Prestosuchus*. A similar situation obtains in the Ischigualasto Formation, where the carnivorous dinosaur *Herrerasaurus* is found with the same size carnivorous thecodont *Saurosuchus*. The earliest ornithischian, *Pisanosaurus*, is found in the Ischigualasto Formation and, although poorly preserved, shows that the basic features of the group had been acquired by that time (Casamiquela, 1967). The first theropods occur at approximately the same time (Charig, 1967), apparently occupying an ecologic role parallel to that of the ornithosuchid thecodonts.

Nevertheless, the thecodonts were considerably more abundant and varied in the sediments of the Middle and lower Late Triassic. They apparently took over the carnivore niche previously occupied by the carnivorous cynodonts, but did not extend into the herbivore field (with the exception of the aetosaurs). Dinosaurs produced both carnivores and herbivores early in their history. The origins of both categories are still virtually unknown.

Actual data from the fossil record allow three well-supported concepts to be stated: 1) dinosaurs were in existence at least during the last half of the Triassic; 2) thecodonts were abundant and diverse during the Middle and first half of the Late Triassic, becoming less so during the latter part of the Late Triassic; 3) although dinosaurs existed earlier, their major expansion

did not begin until the last half of the Late Triassic. The reasons for the difference in expansion phases between the two groups are not clearly understood, nor can the apparent ecologic overlap between the large carnivores be explained on the basis of current data. However, it seems an inescapable conclusion that the more agile mechanical condition of the dinosaur limbs was a factor in their eventual replacement of the thecodonts. It is also possible that the dinosaurs were undergoing more extensive physiologic changes, perhaps related to the changes in locomotion (see Bakker, 1972).

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